The Effect of Novelty on Subsequent Choice and Preferences

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THE EFFECT OF NOVELTY ON SUBSEQUENT CHOICE AND PREFERENCES

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This manuscript examines the effect of a novel experience on subsequent choice and preferences.

Chapter 1 reviews neuroimaging and behavioral evidence suggesting that novelty activates dopaminergic brain areas involved in reward processing and serves as a reward-predicting cue, enhancing responses to the rewarding aspects of stimuli and motivating exploration in search of potentially valuable outcomes. Based on this evidence, it is proposed that people will be more likely to explore, following a novel experience, and that in a consumer context this exploratory tendency will result in choice of a broader and more varied set of options from an assortment of products. Results from three experiments support these hypotheses. Study 1 showed that participants who had seen novel (vs. familiarized) images chose a greater diversity of snacks in a subsequent task and rated those snacks as more appealing. Study 2 conceptually replicated these effects in the context of a series of choices and also showed, consistently with theory and predictions, that the effect of novelty on subsequent variety seeking is observed only when the choice options are potentially rewarding. Study 3 demonstrated that exposure to novelty improves evaluations and promotes exploration among less typical, but still enjoyable, members of a product category, suggesting that novelty may promote other forms of consumer exploratory behavior such as innovativeness.

Chapter 2 provides a comprehensive review of the neuroscience literature on reward processing. It outlines the various components of reward processing, such as pleasure, learning, and motivation, and provides a critical analysis of the existing hypotheses about the role of the neurotransmitter dopamine in these processes and the existence of dedicated reward-processing networks in the brain.

Chapter 3 provides a critical overview of ERP and fMRI evidence for the influence of positive affect on various cognitive processes, such as memory, cognitive flexibility, and creative problem solving, and the mediating role of dopamine in these processes. The neuroimaging data is interpreted in the context of findings from behavioral studies; consistencies and discrepancies between the neuroimaging and the behavioral data are discussed.

BIOGRAPHICAL SKETCH

Guergana Pankova Spassova completed her doctoral studies in marketing at the S. C. Johnson Graduate School of Management, Cornell University. Guergana holds also an M.B.A. degree from the University of California at Riverside, and a Bachelor degree in English Studies from Sofia University, Bulgaria.

I dedicate this work to my advisor, Dr. Alice M. Isen, and to my mother and sister. I would like to thank Dr. Isen for the knowledge and wisdom that she has shared with me with patience and dedication, and for her endless support and optimism. My gratitude also goes to my mother and sister who believed in me and were always there for me, even in the most difficult times.

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CHAPTER 1

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Consumers' product search and decision making often begin with exposure to something novel. For example, the first section that consumers encounter in a clothing store is typically "new arrivals." Similarly, online stores often have information about new products prominently displayed on the home page. And a visit to the grocery store may involve sampling new products or encountering a novel display or décor. Novel items provoke attention, curiosity, and exploration, and these effects have been well documented in the cognitive and social psychology literatures, as well as the marketing literature (Berlyne 1960; Fiske and Maddi 1961; Venkatesan 1973).

The downstream effects of a novel experience on preferences and choice, however, have received little attention. How does a novel experience affect consumers' tendency to explore among subsequent product options? Do they consider a broader, or a narrower, range of options after having browsed through the store's novel items first? Does the novel design of an online store's home page, or a traditional store's décor, influence the range of products consumers purchase, and their liking for these products? We propose that experiencing novelty will lead consumers to explore more in a subsequent situation, and that this exploratory tendency will result in choice of a more varied set of options from an assortment of products.

Theoretical Background

Novelty: Definitions and Types

Researchers have distinguished among several types of novelty. One

distinction is based on temporal considerations: an item can be novel with respect to an individual's recent experience (short-term novelty), more distant experience (long-term novelty), or total experience (complete novelty) (Berlyne 1960; Daffner et al. 2000a). A distinction has also been made between "absolute novelty," when a stimulus has a quality that has never been perceived before, and "relative novelty," when a stimulus possesses familiar qualities but in a novel combination or arrangement (Berlyne 1960), or "associative novelty," when a familiar stimulus is presented in a novel configuration with other stimuli (Lisman and Grace 2005; Schott et al. 2004). Lisman and Grace (2005) have also identified a form of novelty related to events or stimuli that are unexpected under a given cue condition. This is similar to the operationalization of novelty in event-related potential (ERP) studies, where, in an odd-ball paradigm, a novel event is a low-frequency deviant or unexpected stimulus appearing within a train of homogeneous "standard" stimuli (e.g., Friedman et al. 2001). Bunzek and Duzel (2006), however, present fMRI evidence that contextual deviance of this kind does not produce the same brain activity or the same cognitive effects as "pure novelty" (i.e., never-seen-before stimuli). Their view is closer to that of Berlyne (1960), who classifies "surprisingness" together with other stimulus properties such as change, complexity, and incongruity that often accompany novelty, but do not constitute novelty per se.

At this point, there seems to be no agreement as to how exactly the construct of "novelty" should be defined, and whether the different types of novelty identified in the literature are processed in a different manner by the brain and produce distinct cognitive and behavioral effects. Combining imaging techniques, such as ERP and fMRI, with more traditional cognitive and behavioral measures, may shed more light on these issues in the future.

In any case, it is likely that most instances of novelty in one's everyday life

will be of the "short-term," "long-term", or "relative," rather than the "absolute" or "complete" type of novelty, since, as Berlyne (1960) pointed out, however novel a stimulus maybe, it must be "similar to and relatable to a host of familiar and frequently experienced entities" and "must consist of lines, angles, and curves such as have been seen earlier" (Berlyne 1960, p. 25). The extent to which a stimulus is considered novel, then, will likely depend on the individual's subjective past experience, as well as on the particular context in which that stimulus is encountered.

The subjective novelty of a stimulus or configuration has been found to decline progressively with repetition of that stimulus or configuration (e.g., Berlyne and Parham 1968; Daffner et al. 1998), and to increase with the number of repetitions of a stimulus or configuration presented prior to the target one, as well as with the number of properties along which the target stimulus differs from the preceding ones (Berlyne and Parham 1968). Novelty, in its various forms, has also been found to possess certain properties that are of particular relevance to the present research, and are reviewed in the following section.

Properties of Novelty

Novelty, attention, and exploration. Psychologists have long shown that novelty attracts attention and promotes exploratory responses (Berlyne 1960; Chong et al. 2008; Daffner et al. 1998; 2000a; Fiske and Maddi 1961; Mesulam 1998). Berlyne (1960) described a series of experiments showing that people attend preferentially to novel, vs. familiar, stimuli. For example, when a white and a red circle appeared simultaneously in an aperture, a significantly greater percentage of participants responded to the white circle after having viewed a series of red circles earlier, and to the red circle after having viewed a series of white circles. In another experiment, pairs of images were projected on a screen, for 10 seconds each, the same image

appearing repeatedly on one side, and a different image appearing every time on the other side. Participants spent a growing proportion of the 10 seconds fixating the novel slide. Infants have been shown to maintain their gaze for a longer time at novel stimuli when presented within a pair of novel and already viewed stimuli (Fagan 1990), and to be more likely to play with novel than with familiar toys (Fiske and Maddi 1961). Similar results, using viewing time as a measure of attention and exploration, have been reported in a number of more recent studies as well (e.g., Chong et al. 2008; Daffner et al. 1998; 2000a). Marketing researchers have also noted the importance of novelty, in the form of new products, new ads, etc., in capturing the attention of consumers (Faison 1977; Hirschman 1980; Howard and Sheth 1969; Raju 1980; Venkatesan 1973). Hirschman (1980), for example, pointed out that it is the propensity of consumers to adopt new products such as new ideas, goods, or services, "that gives the marketplace its dynamic nature," and without which "consumer behavior would consist of a series of routinized buying responses to a static set of products" (Hirschman 1980, p. 283).

At the physiological level, the link between novelty, attention, and exploration is supported by ERP studies of the "orienting response" to novel stimuli. The most commonly studied ERP responses to novelty are the N2 and the P3. The N2 is a negative deflection in the brain's electrical field that is evoked in the 180-325 ms temporal window. It is sensitive to deviations from long-term context that render a stimulus unfamiliar and difficult to encode (i.e., strange and unusual visual patterns). The P3 is a positive deflection that peaks at about 300 ms after stimulus onset and is evoked in all three primary sensory modalities in response to infrequent, novel stimuli that deviate from the immediate context (Daffner et al. 2000b). In addition to reflecting the processing of different aspects of novelty (i.e. novelty with respect to long-term context vs. novelty with respect to immediate or local context), the N2 and

the P3 also are believed to differ in the level of cognitive resources involved. While the N2 is considered to be preattentive, relatively automatic and involuntary, the P3 is believed to mark the preferential allocation of attentional resources to potentially significant events and to be modulated by a variety of factors such as task relevance and subjective motivation (Chong et al. 2008). This is supported by observed strong correlation between the amplitude of the P3 response to a stimulus and the duration of viewing of that stimulus (Daffner et al. 1998). The P3, furthermore, involves two subcomponents: an earlier anterior P3a and a later posterior P3b. It is believed that the P3a indexes decisions about the extent to which novel or deviant stimuli or events are potentially significant and merit the allocation of additional processing resources, while the P3b indexes the process of updating representations in working memory and categorizing the novel stimulus (Chong et al. 2008). Both N2 and P3 diminish in amplitude with repeated exposure to the novel stimulus (Daffner et al. 1998), reflecting the process of habituation.

Novelty and learning. Besides facilitating attention, novelty is also believed to represent a potent encoding signal. According to Tulving's "novelty/encoding hypothesis" (Tulving et al. 1996), for example, the probability of long-term encoding of information is directly related to the degree of its novelty. Tulving postulated the existence of a dedicated novelty assessment network in the brain that identifies adaptively significant novel events and stimuli and transmits the relevant information for further processing.

The components of this network are now relatively well understood. It is believed that novelty is first assessed in the hippocampus, where incoming information is compared with stored memories (Lisman and Grace 2005; Grace et al. 2007). The novelty signal is then carried from the hippocampus to the Ventral Tegmental Area (VTA) along a polysynaptic pathway through the nucleus accumbens

(NAc) and the ventral pallidum. A population of dopamine (DA) neurons in the VTA is held at a constant hyperpolarized, inactive state by the ventral pallidum. Inactivation of the ventral pallidum by the NAc releases the VTA DA neurons from inhibition and allows them to enter a state of spontaneous "tonic" firing activity. The transition from this "tonic" state to a burst-firing "phasic" dopamine response depends on input from the pedunculopontene tegmentum (PPTg) – a structure that receives various sensory inputs, as well as inputs from the prefrontal cortex (PFC) and limbic structures such as the amygdala (Grace et al. 2007). Thus the novelty signal from the hippocampus is modulated by goal-related, affective, and sensory information (Grace et al. 2007; Lisman and Grace 2005), and this modulation determines the phasic firing of the DA neurons in the VTA. The VTA then sends ascending projections back to the hippocampus, among other structures, completing the hippocampal – VTA loop and allowing the novel information to enter long-term memory. It is now well established that the dopamine released into the hippocampus by the firing VTA DA neurons, following exposure to novelty, enhances long-term potentiation and promotes learning (Grace et al. 2007; Li et al. 2003; Lisman and Grace 2005).

Novelty and reward. It has been suggested that the preferential attention, exploration, and encoding of novel stimuli may be part of an adaptive mechanism facilitating the learning of new sources of reward (Kakade and Dayan 2002; Krebs et al. 2009; Wittmann et al. 2008). Some researchers, in fact, hold the view that novelty may have intrinsically rewarding properties, as suggested by findings in the animal literature showing that novelty can reinforce and maintain behavior and produce preferences for places associated with it (Bevins et al. 2002; Butler 1953). Monkeys, for example, successfully learned an object discrimination task in a setting where the only reward was visual exploration (Butler 1953) and rats developed conditioned preferences for places associated with access to novel objects (Bevins et al. 2002).

The view that novelty is rewarding is also supported by findings that, in both animals and humans, exposure to novel stimuli is associated with activity in reward-processing dopaminergic areas such as the substantia nigra/ventral tegmental area (SN/VTA) and NAc (Bunzeck and Duzel 2006; Fenker et al. 2008; Krebs et al. 2009; Wittmann et al. 2008). Specifically, midbrain dopaminergic neurons that respond preferentially to rewards and reward-predicting cues, also get activated by affectively neutral novel stimuli (Bunzeck and Duzel 2006; Ljungberg, Apicela, and Schultz 1992; Schultz 1998) and by associative novelty (Schott et al. 2004). Furthermore, in a paradigm modeled under classical conditioning procedures, a familiar cue predicting subsequent novelty itself activates midbrain dopamine neurons, similarly to the way in which these neurons get activated by reward-predicting cues (Wittmann et al. 2007).

The view that novelty may be intrinsically rewarding runs counter to the "mere exposure" effect, suggested by Zajonc (1968), which argues that liking increases with familiarity. In his seminal paper, Zajonc (1968) showed that people rated various stimuli, such as "Turkish" words, Chinese characters, and photographs of men, more positively after repeated exposure. This effect was subsequently replicated over a wide range of stimuli including music, paintings, drawings, photographs, words, ideographs, as well as real people and objects (for a review, see Bornstein 1989).

The conflicting findings regarding the affective value of novelty can be partially reconciled, when certain moderating factors are taken into account. Specifically, according to the two-factor model by Berlyne (1970), exposure effects are driven by two parallel processes – habituation and tedium, and are moderated by the nature of the exposure sequence (e.g., homogeneous vs. heterogeneous) and the complexity of the target stimuli. Monotonous and homogeneous sequences are more conducive than varied sequences to a decline in affective value after familiarization. Furthermore, the perceived value of complex stimuli tends to increase with repetition,

due to the prevalence of the habituation factor, but the value of simple stimuli decreases, due to the prevalence of tedium. Berlyne's two-factor model has been supported by a number of studies across a range of stimuli (for a summary see Bornstein 1989), including advertising messages and consumer products (Anand and Sternthal 1990; Cox and Cox 1988; Mukherjee and Hoyer 2001).

Recent findings reported in the cognitive neuroscience literature suggest that responses to novelty may also depend on the relevant context. There is evidence that in contexts that hold the potential for reward, novelty serves as a reward-predicting cue that enhances the salience of rewards and motivates the organism to explore in search of valuable outcomes (Krebs et al. 2009; Wittmann et al. 2008). In a study by Wittmann et al. (2008), for example, participants engaged in an appetitive reinforcement learning task involving choice from options associated with specific reward probabilities. The choice options on each trial were represented by four simultaneously presented images and each image was associated with a constant probability of earning money. Participants learned an option's reward probability by repeatedly sampling it, over a course of 20 choice trials. Importantly, participants were familiarized with half of the images (though not with their associated reward probability) prior to the choice task, and the other half of the images were new. The novelty of the images was manipulated independent of their reward probability. Results showed that in the initial stages of the learning task, participants were significantly more likely to choose novel images over familiar ones i.e., participants behaved as if the expected monetary value of novel images was significantly higher than the expected value of familiarized ones.

In a similar experimental paradigm, Krebs et al. (2009) showed that choice of new (vs. familiarized) images that predicted subsequent reward was associated with significantly stronger activity in reward-processing dopaminergic areas such as the

SN/VTA and the NAc. This pattern of results is consistent with computational choice models in which the value of exploration is represented by assigning fictitious "bonus" reward value to novel choice options (Kakade and Dayan 2002).

Importantly, there is initial evidence that novelty enhances reward expectations not only with regard to the novel items themselves, but also with regard to items encountered in a subsequent situation (Guitart-Masip et al. 2010). In an fMRI study, participants were first presented with either novel or with previously seen (familiarized) images of indoor or outdoor scenes. Afterwards, they engaged in an unrelated task in which a different set of images (abstract patterns) served as cues predicting the receipt of monetary reward, under different probabilities. The fMRI data revealed that, relative to participants who had viewed familiarized indoor/outdoor images, participants who had viewed novel indoor/outdoor images exhibited higher activity in reward-related brain areas (i.e., the striatum) during the subsequent reward task. The authors concluded that novelty enhances reward responses even when novelty and reward constitute unrelated, independent events (Guitart-Masip et al. 2010). These findings are consistent with the physiological model by Lisman and Grace (2005), described earlier, in which novelty exposure boosts subsequent phasic dopaminergic responses to rewards by inducing tonic activity in previously inactive VTA dopamine neurons. The results are also consistent with temporally-extended contextual effects of novelty exposure reported in the literature on memory and learning **(**Bunzek and Düzel 2006; Davis, Jones, and Derrick 2004; Fenker et al. 2008), where exposure to novelty has been found to promote the encoding of unrelated, subsequently encountered stimuli.

In summary, the literature on novelty suggests that novelty promotes attention, exploration, and learning, and that these effects are at least in part driven by a mechanism in which novelty serves as a reward-predicting cue motivating exploration

in search of potentially valuable outcomes. Importantly, there is initial evidence that novelty may also have important contextual effects, such as enhancing reward-predicting responses to subsequently encountered stimuli (Guitart-Masip et al. 2001).

Research Hypotheses

Based on the above reviewed properties of novelty, we propose that the ability of novelty to promote exploration in search of potentially rewarding outcomes extends beyond the novel items, to subsequently encountered unrelated items. Specifically, we propose that people will be more likely to explore after experiencing something novel, as long as the novelty is not perceived as negative. We test this proposition in a consumer context.

In a consumer context, the tendency to explore may be reflected by curiosity-motivated information seeking (e.g., information search about products or services), variety seeking (e.g., a tendency to seek diversity in product choice), or innovativeness (e.g., trial or adoption of new products) (Raju 1980; Steenkamp and Baumgartner 1992). The current paper investigates of the effect of novelty on consumer variety seeking and begins investigation of its effect on innovativeness.

Variety-seeking has been a central area of research in marketing (for a review, see McAlister and Pessemier 1982). Variety-seeking can arise both over time, when consumers choose different options on successive occasions (e.g., Givon 1984; Kahn, Kalwani, and Morrison 1986), and when they choose a portfolio of options on a single occasion (e.g., Simonson 1990). Two major types of drivers of variety-seeking behavior have been identified: external drivers, such as sales, promotions, or out-of-stock conditions, and internal drivers such as consumers' desire for variety, stimulation, or novelty (for a review, see Kahn 1995; McAlister and Pessemier 1982). A number of variables moderating consumers' desire for variety have been

investigated, from personality characteristics, such as one's optimum level of stimulation (Baumgartner and Steenkamp 1996; Raju 1980; Steenkamp and Baumgartner 1992), to contextual factors such as the consumption setting (e.g., public vs. private; Ariely and Levav 2000), the timing of choice and consumption (e.g., simultaneous vs. sequential; Simonson 1990), the variety provided by the context (Menon and Kahn 1995), and the affective state of the consumer (Kahn and Isen 1993).

We propose that consumers' propensity to seek variety will also be moderated by prior exposure to novelty. Specifically, we test the hypothesis that encountering novelty will promote diversity in subsequent product choice.

Research on innovativeness, at the individual consumer level, has focused mostly on the influence of demographic variables and personality characteristics on consumers' propensity to try or adopt new products (Baumgartner and Steenkamp 1996; Herzenstein, Posavac, and Brakus 2007; Raju 1980; Steenkamp and Baumgartner 1992; Steenkamp and Gielens 2003). The influence of moderators such as prior knowledge (Moreau, Lehmann, and Markman 2001), temporal distance (Castano et al. 2008), and positive affect (Barone, Miniard, and Romeo 2000; Kahn and Isen 1993) has also been investigated.

We propose that consumers' propensity to innovate will also be affected by prior exposure to novelty. Specifically, we test the hypothesis that encountering novelty will promote willingness to try new or unusual options in subsequent product choice.

In summary, we propose that encountering novelty in one situation will promote subsequent exploration, and that in a consumer context this exploratory tendency will be reflected in greater diversity in product choice, as well as in higher likelihood of trying new or unusual product options.

Study 1

Method

Thirty-nine university students participated in this study, with eighteen of them randomly assigned to a novelty condition, and the rest to a control condition.

Novelty manipulation. Novelty in this study was operationalized as the appearance of novel stimuli at the end of a series of repeating, familiarized stimuli in a product-ranking task. Specifically, participants viewed a series of twelve sets of product images on the computer and ranked the four images in each set for personal preference. In the control condition, the images in all twelve sets were of Tide laundry detergent. There were eight different types (e.g., Tide with Dawny, Tide with Febreze, etc.), and each type was repeated six times over the course of the twelve trials. In the novelty condition, the images in the first eleven sets were the same as those in the control condition, but the images in the last set were new and were also from a different product category (Crest tooth paste). This operationalization of novelty is similar to that in Berlyne's studies (Berlyne 1970), where an item is judged to be more novel when it appears at the end of a sequence of repeating items and differs from those preceding items along several dimensions.

All images were pretested for valence and arousal with a group of 62 students recruited from the same pool as participants in the main study. Participants in the pretest indicated how each of the images made them feel on seven-point scales measuring valence (bad/good, unpleasant/pleasant, negative/positive; valence index, α = .98) and arousal (peaceful/nervous, relaxed/tense, r = .93). Repeated-measures ANOVAs indicated that the Tide detergent images did not differ, on average, from the Crest toothpaste images in valence (M = 5.42 vs. 5.39; $F(1, 61) < 1$, NS) or arousal (M

= 2.88 vs. 2.73; $F(1, 61) < 1$, NS).

Procedure. Participants were run one at a time. Each performed two tasks, the product ranking task, which was also the novelty manipulation, and then a snack choice task which took place in a separate room. Participants were told that the management of a cafeteria wanted to know what kinds of snacks were popular among students. Every participant received $3.00 which could be used to purchase items from a set of twelve snacks (*Coke, Tropicana orange juice, Snyder's pretzels, Doritos tortilla chips, Snickers candy bar, M&Ms chocolate candies, Nature Valley granola bar, Welch's dried fruit, Milky Way candy bar, Kit-Kat candy bar, Almond Joy candy bar, and Minute Maid raisins*). All snacks were displayed on a table, with the price clearly indicated. Prices of the different items ranged from $0.50 to $1.50. Participants could purchase any combination of snacks within their $3.00 budget, including multiples of the same snack, or no snacks at all. The number of different snacks participants purchased served as a measure of variety seeking in this context (Simonson 1990). Participants also indicated how much they liked the snacks, how attractive, and how tempting the snacks were, on seven-point scales (1 = not at all; 7 = extremely).

Results and Discussion

A one-way ANOVA revealed that participants in the novelty and control conditions did not differ significantly in the average total number of snacks purchased ($M_{novelty}$ = 3.11 vs. $M_{control}$ = 2.24; $F(1, 37) = 2.43$, $p = 1.13$). However, a one-way ANOVA on the number of *different* snacks purchased revealed that novelty participants chose a significantly more varied snack portfolio than did controls ($M_{novelty}$ = 3.00 vs. $M_{control}$ = 1.76, $F(1, 37) = 7.45$, $p = .01$). While controls tended to purchase more of the same snack (e.g., four cans of Coke), novelty participants purchased a

more diverse set of snacks. We created a "snack appeal" index ($\alpha = .85$), combining the three questions regarding the attractiveness of the snacks. A one-way ANOVA on this index revealed that novelty participants perceived the set of snacks as significantly more attractive ($M = 5.07$) than did controls ($M = 3.97$; $F(1, 37) = 6.82$, $p = .01$).

To test whether the enhanced appeal of the snacks mediated the effect of novelty on the diversity of the snacks chosen, a mediation analysis was performed following the Baron and Kenny (1986) procedure. The first criterion for mediation was satisfied because, when the snack appeal index was regressed on novelty, the coefficient for novelty was significant ($\beta = 1.11$, $t = 2.61$, $p = .01$). The second criterion was also satisfied because, when the diversity measure was regressed on the snack appeal index, the coefficient for the index was also significant ($\beta = .67$, $t = 4.78$, $p < .0001$). The third and final criterion was supported because the effect of novelty on diversity, which was significant when diversity was regressed on novelty alone ($\beta = 1.24$, $t = 2.73$, $p = .01$), became non-significant when the snack appeal index was included in the model ($\beta = .59$, $t = 1.41$, $p > .10$), but the coefficient for the snack appeal index remained significant ($\beta = .58$, $t = 3.89$, $p < .0001$). The drop in significance level for the effect of novelty on diversity was significant (Sobel $z = 2.31$, $p = .02$). Thus the increased appeal of the snacks resulting from novelty mediated novelty's effect on the preference for diversity.

This study provided initial support for our hypothesis that novelty promotes subsequent exploration manifested as preference for diversity. Participants who viewed a series of images containing novelty selected more different options in a subsequent choice task. They also rated the choice options as more appealing, and this enhanced appeal mediated the influence of novelty on preference for diversity. The data is also consistent with the view that novelty promotes exploration by enhancing the salience of the potentially rewarding properties of options.

One could argue, however, that novelty in our manipulation was confounded with variety since the set of product images in the novelty condition was also more varied than that in the control condition. This higher variety, not novelty, may have prompted participants to choose more varied items later on, which would be consistent with the findings by Maimaran and Wheeler (2008) who show that exposure to arrays of geometric figures characterized by variety primes variety seeking in a subsequent unrelated choice task. To rule out priming as an alternative explanation, we used a different manipulation of novelty in our next studies. We also tested a boundary condition for the predicted effect: we reasoned that if the effect of novelty on choice diversity was the result of an enhanced expectation of rewards, it should be observed only when the options available for choice were attractive (i.e., when there was a possibility for reward). If the effect, however, is due to priming, it should be observed regardless of the attractiveness of the choice options.

Study 2

Study 2 was designed to replicate conceptually the effect of novelty on preference for diversity observed in study 1, using a different manipulation of novelty. It also included another measure, typically used in the variety-seeking literature, namely switching among choice options over time, in order to see whether the effect of novelty is specifically on diversity, or if it applies to variety-seeking more broadly, as it has been studied in the literature (Givon 1984; Kahn, Kalwani, and Morrison 1986; McAlister and Pessemier 1982). Study 2 also tested whether the effect of novelty on variety seeking is moderated by the attractiveness of the options available for choice. For this purpose, we created two sets of choice options – a more appealing one, and a less appealing one. We predicted that novelty would promote variety

seeking when participants chose from the more appealing set of options, but not when they chose from the less appealing set.

Method

One hundred university students participated in this study, which used a 2 (novelty: novelty vs. control) x 2 (choice set: more appealing vs. less appealing) between-subjects design.

Novelty manipulation. Novelty in this study was manipulated using a word task. Participants were asked, at the beginning of the session, to write down the first associate that came to mind in response to each of nine words, pretested to be different in familiarity, but equivalent in valence (neutral) and arousal. In the control condition, participants provided associates to nine common, neutrally-valenced words (e.g., building, paper, etc.), and in the novelty condition to nine less familiar, neutrally-valenced words (e.g., marmot, dais, etc.).

In a pretest conducted with 58 students from the same population as those in the main study, the novelty and control words were selected from an initial set of 75 words. Pretest participants rated the familiarity of each word using two seven-point semantic differential scales (unfamiliar-familiar, unusual-common; $r = .91$). Participants also indicated how each of the words made them feel on four seven-point valence scales (sad-happy, unpleasant-pleasant, negative-positive, bad-good; valence index, $\alpha = .99$) and three seven-point arousal scales (peaceful-nervous, relaxed-tense, calm-afraid; arousal index, $\alpha = .97$). Based on the pretest results, eighteen words (nine control and nine novelty words) were selected for use in the word-associates task that was to constitute the novelty manipulation. The novelty words were rated as significantly less familiar ($M_{novelty} = 2.14$ vs. $M_{control} = 5.11$; $F(1, 56) = 67.59$, $p < .001$), but not significantly different in terms of valence ($M_{novelty} = 3.09$ vs. $M_{control} =$

3.11; $F(1, 56) = .08$, NS) or arousal ($M_{novelty} = 3.02$ vs. $M_{control} = 2.97$; $F(1, 56) = .48$, NS).

Choice-set manipulation. Two different snack choice sets were created: a more appealing one (*Lay's potato chips, Cheetos cheese snacks, Doritos tortilla chips, Chex Mix party mix, RoldGold pretzels,* and *Smartfood popcorn)* and a less appealing one, containing two of the snacks from the appealing set *(RoldGold pretzels,* and *Smartfood popcorn)* and four "negative" snacks (*Lay's fried pork rinds, Ruffle's dill pickle chips, Genisoy's low-salt soy sticks, Lowry's deep fried bacon curls),* based on a pretest with 107 participants from the same population as those in the study. Participants in the pretest rated the taste of each snack on a 7-point scale (1 = very bad taste, 7 = very good taste). A repeated-measures ANOVA showed that the snacks in the less appealing set were perceived as significantly worse tasting (M = 3.14), on average, than the snacks in the more appealing set, ($M = 5.16$; $F(1, 115) = 144.03$, $p < .001$).

Procedure. First, participants performed the word-associates task, which constituted the novelty manipulation, but was described as a pretest of materials to be used in future studies. The associates provided by the participants in response to these words would later be evaluated for unusualness and for valence by independent judges, to constitute an implicit manipulation check. Then participants were given a choice task, which involved the dependent measures for the study. Participants were asked to assume that they would be on campus the following ten days and that each day they would purchase one snack from a vending machine. The snacks available on each day were listed on the computer screen. Half of the participants chose from the more appealing choice set, and the other half from the less appealing set. The main dependent variable was variety seeking assessed as the number of different snacks (diversity) participants included in their choice portfolio and the number of times they switched from one snack to another (switching). Participants also indicated, on three

7-point scales, how much they found the snacks to be attractive, appealing, and liked (1 = not at all, 7 = a lot; snack appeal index, $\alpha = .86$).

Results

Manipulation check. To assess the effectiveness of the novelty manipulation, we analyzed the unusualness of the associates that participants gave in the word task, because prior research has shown that novel, relative to familiar, words elicit more diverse and unusual associations (Cramer 1968). To assess unusualness, we calculated, for every participant, the mean number of other respondents who gave the same associate, averaging over the ten words. A one-way ANOVA revealed that this mean was significantly lower in the novelty condition than in the control condition, i.e., fewer identical responses were generated in the novelty condition than in the control condition ($M_{novelty} = 6.06$ vs. $M_{control} = 11.37$; $F(1, 98) = 60.47$, $p < .001$).

To verify that the novelty words did not differ, on average, from the control words in terms of valence, two judges, blind to the study hypotheses and the subject's experimental condition, rated the associates given by the participants in response to the stimulus words in terms of positivity and negativity. The ratings by the two judges were significantly correlated ($r = .85$) and found no difference between the novelty and control conditions in the valence of their associates ($M_{control} = .06$ vs. $M_{novelty} = .02$; $F(1, 98) < 1$, *NS*).

Variety-seeking. A 2 (novelty: novelty vs. control) x 2 (choice set: more appealing vs. less appealing) ANOVA on the number of different snacks participants chose over the ten trials revealed a main effect of choice set, $F(1, 96) = 15.11$; $p < .001$. Participants chose more different items from the more appealing set ($M_{more\ appealing} = 4.13$ vs. $M_{less\ appealing} = 3.30$). This main effect was qualified by a significant interaction between novelty and choice set ($F(1, 96) = 4.52$, $p < .05$). Planned

contrasts revealed that novelty participants selected a significantly higher number of different snacks when choosing from the more appealing set ($M_{novelty}$ = 4.56 vs. $M_{control}$ = 3.75; $F(1, 96) = 7.11$, $p = .01$), but not when choosing from the less appealing set ($M_{novelty}$ = 3.23 vs. $M_{control}$ = 3.36; $F(1, 96) < 1$, NS) (see Figure 1 below).

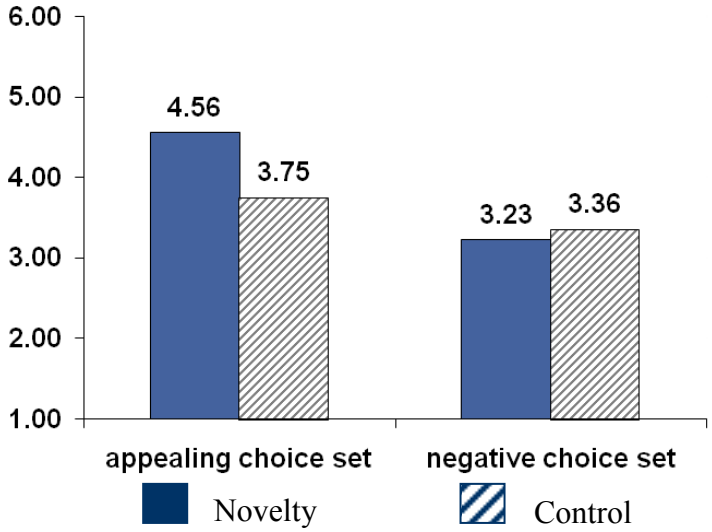

Figure 1: Number of different snacks chosen (study 2).

A 2 (novelty) x 2 (choice set) ANOVA on the number of consecutive switches found no significant main effects of choice set ($F(1, 96) = 2.82$, $p = .10$) or novelty ($F(1, 96) < 1$, NS), nor a significant interaction between the two variables ($F(1, 96) = 1.11$, $p = .30$).

Snack appeal. Next, we examined participants' ratings of the snack attractiveness. A two-way ANOVA on the snack-appeal index revealed a main effect of choice set, $F(1, 96) = 103.84$, $p < .0001$. Participants liked the snacks in the more appealing set significantly more (M = 4.70) than those in the less appealing set (M = 2.82). There was also a significant main effect of novelty, $F(1, 96) = 8.10$, $p = .005$. Novelty participants perceived the snacks as significantly more appealing ($M_{novelty}$ = 4.11 vs. $M_{control}$ = 3.55). These main effects were qualified again by a significant

interaction between choice set and novelty, $F(1, 96) = 4.89$, $p < .05$. Planned contrasts clarified that novelty participants perceived the snacks in the more appealing set as more attractive than did controls ($M_{novelty} = 5.20$ vs. $M_{control} = 4.25$, $F(1, 96) = 13.70.$, $p < .001$) but did not differ from controls on the less appealing set ($M_{novelty} = 2.88$ vs. $M_{control} = 2.76$, $F < 1$, NS) (See Figure 2 on next page).

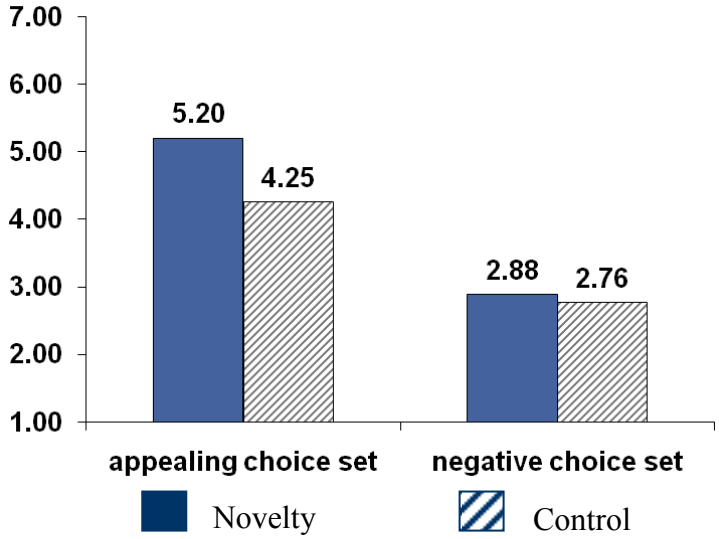

Figure 2: Snack appeal (Study 2)

Discussion

Study 2 replicated the effect of novelty on the diversity of subsequent choice observed in study 1, using a different novelty manipulation. People exposed to unfamiliar words selected a more diverse range of snacks in a following choice task, and also rated these snacks more positively. Importantly, these effects were moderated by the attractiveness of the available options. When the choice set contained, on average, less appealing snacks, novelty participants did not differ from controls in the diversity of their choice, or in the perceived attractiveness of the options.

This data speaks against a simple priming account for the observed effect of novelty. If exposure to novelty primed the semantic concept of novelty or a behavioral

goal to choose more novel or diverse items, then the effect would have been observed when the choice items were less attractive, as well as when they were more attractive. Instead, our findings fit with the view that novelty promotes exploration in search of potentially rewarding options.

We observed an effect of novelty only on the diversity-of-choice measure, and not on switching. Our hypotheses are focused on exploration, and thus diversity of the selected options is a better measure of exploration than switching. While one may switch among options simply to reduce boredom or satiation, more diverse choices may indicate a tendency to try more novel or unusual things (i.e., explore). The next study tests this proposition.

Study 3

Study 3 was designed to test whether prior exposure to novelty prompts people not only to choose more diverse options but also to try more unusual options.

Method

Forty-nine university students participated in this study, which used a 2 (novelty: novelty vs. control) x 2 (snack type: typical snacks vs. unusual snacks) mixed-factor design, with novelty as a between-subjects factor, and snack type as a within-subjects factor.

Novelty Manipulation. Novelty was manipulated through a word task, as in study 2.

Snack type manipulation. The context for the choice task in this study was again choice of a vending-machine snack. To test our idea that the experience of

novelty may prompt exploration (i.e., trying unusual items), half of the snacks in the choice set were typical vending-machine snacks (*Lay's potato chips, RoldGold pretzels, Welch's dried fruit snack*), and the other half were unusual (*Danon fruit-on-the bottom yogurt, Quaker instant cereal, Campbell's microwavable soup*) for the context. The unusual snacks did not differ from the typical ones in terms of taste ratings ($M_{typical}$ = 4.95 vs. $M_{unusual}$ = 4.46, $F(1, 52) = 1.65$, $p > .20$), based on a pretest with 53 students from the same population as those in the main study.

Procedure. Participants performed two tasks, both on computer: first the word-associates task, which contained our manipulation of novelty, and then a choice task. In the choice task, participants were asked to assume that they were buying snacks from a vending machine and had to choose one from a set of six snacks, to have on each of the following ten days. Three of the snacks were the typical vending-machine snacks, and the other three were the less typical, as described earlier. The number of different items participants selected over the course of the ten choice trials served as a measure of choice diversity. After making the choices, participants were asked to indicate, for each of the six snacks in the choice set, how appealing that snack was (1 = not at all appealing, 7 = very appealing), the degree to which it was a typical vending machine snack (1 = not at all typical, 7 = very typical).

Results

Manipulations checks. The success of the novelty manipulation was assessed as described in study 2. An ANOVA revealed that significantly fewer participants in the novelty condition gave identical associates than in the control condition ($M_{novelty}$ = 2.59 vs. $M_{control}$ = 6.26; $F(1, 47) = 95.79$, $p < .001$). Furthermore, the associates provided by participants in the novelty condition did not differ significantly in valence

from those provided by controls ($M_{novelty}$ = .17 vs. $M_{control}$ = .02; $F(1, 48) = 1.19$, $p >$ .20).

Success of the typicality manipulation was established by averaging participants' ratings of the representativeness of the two groups of snacks: chips, pretzels, and dried fruit (typical vending machine snack index, α = .60), and yogurt, cereal, and soup (unusual vending machine snack index, α = .66), as members of the category "vending machine snack." A mixed-factor ANOVA with novelty as a between-subjects factor and snack type as a within-subjects factor revealed only a main within-subjects effect of snack type, ($F(1, 47) = 70.72$, $p < .0001$). Yogurt, cereal, and oatmeal were rated as significantly less typical as vending machine snacks (M = 2.58) than chips, pretzels, and dried fruit (M = 5.39). Neither novelty ($F(1, 47) <$ 1, NS), nor the interaction between snack type and novelty ($F(1, 47) < 1$, NS) was significant.

Variety-seeking. A mixed ANOVA with the novelty manipulation (control words vs. novel words) as a between-subjects factor and the type of snack (typical vs. unusual) as a within-subjects factor, assessing the number of different snacks chosen, revealed two main effects, one of snack type ($F(1, 47) = 8.05$, $p < .01$), and one of novelty, $F(1, 47) = 8.01$, $p < .01$). Participants chose more different options from the typical snacks (M = 2.35) than from the unusual snacks (M = 1.88), and novelty participants chose more different snacks, overall, (M = 2.38) than did controls (M = 1.84). The interaction between novelty and snack type was not significant, ($F(1, 47) <$ 1, NS), but planned contrasts were carried out to evaluate our hypotheses. These revealed that, unlike controls, novelty participants did not differ in their choice of snack as a function of snack type ($M_{unusual}$ = 2.20 vs. $M_{typical}$ = 2.56; $t(49) = 1.36$, $p =$ .18). Furthermore, novelty participants chose more varied snacks than did controls, both when choosing from the typical snacks ($M_{novelty}$ = 2.56 vs. $M_{control}$ = 2.13, $t(47) =$

1.86, $p < .05$) and when choosing from the unusual snacks ($M_{novelty} = 2.20$ vs. $M_{control} = 1.54$, $t(47) = 2.40$, $p = .01$) (See Figure 3 below).

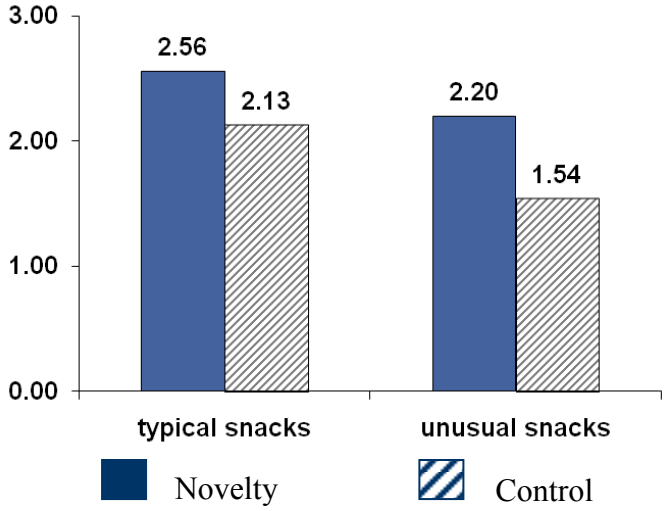

Figure 3: Number of different snacks chosen (Study 3)

A one-way ANOVA showed no significant difference in the number of times novelty participants switched among snacks ($M_{novelty} = 8.36$ vs. $M_{control} = 7.50$; $F(1, 47) = 2.88$, $p = .10$)

Snack appeal. A mixed ANOVA with the novelty manipulation as a between-subjects factor and type of snack as a within-subjects factor, assessing the perceived appeal of the snacks, revealed a main effect of snack type; participants perceived the typical snacks as more appealing ($M = 5.24$) than the less typical snacks ($M = 4.64$; $F(1, 47) = 11.55$, $p = .001$). This main effect, however, was qualified by a significant interaction between the novelty induction and snack type ($F(1, 47) = 4.22$, $p = .05$). Planned contrasts revealed that the interaction was driven by only control participants' ratings of the unusual snacks. Controls rated these snacks as significantly less appealing ($M = 4.32$) than the typical ones ($M = 5.29$; $t(47) = 3.36$, $p = .001$), but novelty participants' ratings of the snacks' attractiveness were not influenced by

typicality ($M_{nontypical}$ = 4.95 vs. $M_{typical}$ = 5.19; $t(48) < 1$, NS). Furthermore, novelty participants' ratings of the unusual snacks were significantly higher than those of controls ($M_{novelty}$ = 4.95 vs. $M_{controls}$ = 4.32; $t(48) = 2.22$, $p < .05$), whereas their ratings of the typical snacks did not differ from controls'($M_{novelty}$ = 5.19 vs. $M_{control}$ = 5.29; $t(49) < 1$, NS) (See Figure 4 below).

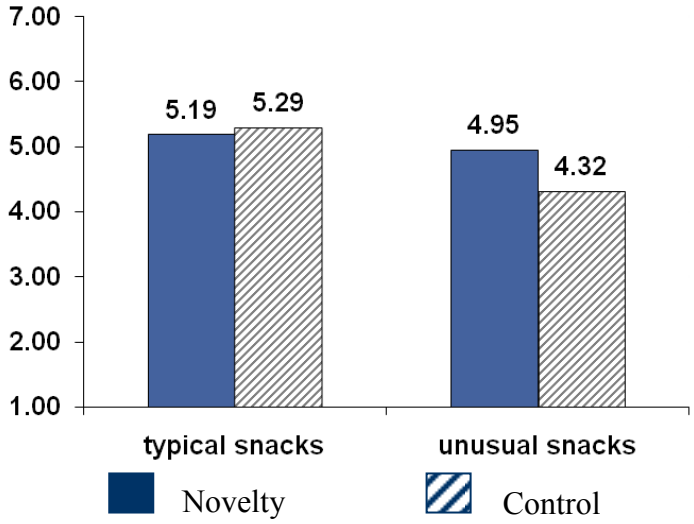

Figure 4: Snack appeal (Study 3)

Discussion

In this study, participants chose from a set of snacks that were all enjoyable, but half were typical vending machine snacks, while the other half were less typical. The typicality of the snacks affected control, but not novelty, participants' choices and evaluations: controls rated the unusual vending machine snacks as less appealing than the typical ones and included fewer of them in their choice portfolio. Participants who had previously been exposed to novel words, in contrast, evaluated the less typical snacks as favorably as the typical ones, and included just as many of them in their choice portfolio. Novelty participants selected more diverse snacks, overall, than controls. This implies that prior exposure to novelty makes people more likely to try

more unusual options, as long as these options are attractive. They explore more among the unusual items, as well as among the typical ones. This also provides initial evidence that exposure to novelty may promote other types of consumer exploratory behavior such as innovativeness.

As in study 2, we did not find an effect of prior novelty exposure on the number of times participants switched among options in the choice task. Both diversity of choice and switching have been used as measures of variety-seeking in the literature. However, it is possible that the choice diversity measure taps more directly into exploratory behavior and willingness to try new options, while one may alternate among options simply to reduce boredom.

General Discussion

The studies reported in this paper tested the hypotheses that exposure to novelty promotes exploration, manifested as choice of more diverse product options or as willingness to try more novel or unusual production options. Supporting this hypothesis, study 1 showed that participants who had engaged in a task involving novel images subsequently selected more diverse options from a set of snacks. Novelty participants also rated the snacks as significantly more appealing, and this enhanced appeal mediated the effect of novelty on choice diversity. Study 2 replicated these effects in the context of a series of choices, using a different novelty manipulation. It also demonstrated a boundary condition for the hypothesized effect of novelty on exploration, namely that this effect is observed only when the choice options are potentially rewarding. Participants who had provided associates to unfamiliar words (vs. familiar words), subsequently chose more diverse snacks, but

only when the snacks were appealing. When the perceived appeal of the snacks was limited, novelty participants did not differ significantly from controls in the diversity of their choice. Finally, study 3 demonstrated that exposure to novelty improves evaluations and promotes exploration among less typical, but still enjoyable, members of a product category, suggesting that novelty may also promote innovative consumer behavior.

We did not find an effect of novelty exposure on the other measure of variety seeking, i.e. switching among options in the choice set. As mentioned earlier, it is possible that choice diversity is a better measure of exploratory behavior than switching. While one may switch among familiar options to reduce boredom, a broader range of choices may indicate willingness to try something new.

Recent findings in the cognitive neuroscience literature suggest that novelty may serve as a reward-predicting cue that motivates exploration in search of valuable outcomes and that novelty amplifies reward signals in the brain (Guitart-Masip et al. 2010; Krebs et al. 2009; Wittmann et al. 2008). Our finding that novelty improves evaluations and exploration among enjoyable product options, but not among unenjoyable ones, is in line with this view.

An alternative explanation for the effects we observed involves the notion of cognitive flexibility. Exposure to novelty has been linked reliably to increased levels of the neurotransmitter dopamine (see Schultz 1998 for a review). Increased levels of dopamine, on the other hand, have been associated with enhanced cognitive flexibility (e.g., Ashby, Isen, and Turken 1999; Cohen, Braver, and Brown 2002). Evidence is accumulating that exposure to novelty improves cognitive flexibility and learning (Davis, Jones, and Derrick 2004; Yerys and Munakata 2006). It is possible that enhancement in cognitive flexibility accounts, at least in part, for the effects observed in our studies. It may explain why, in study 3, participants who were exposed to novel

words, were later significantly more accepting of less typical members of the target product category. The choice of more diverse options may also indicate greater cognitive flexibility, if it reflects a tendency to deviate from habitual choice patterns. An interesting test of this hypothesis might be to measure the extent to which one's choices following novelty are likely to provide a habitual vs. an innovative response.

The effects of novelty on choice diversity, observed in our studies, suggest parallels with the effects of positive affect on variety seeking. As we found for novelty, positive affect has been found to promote variety seeking among safe, enjoyable product options and to improve category-fit evaluations of less typical members of a category (Isen and Daubman 1984; Kahn and Isen 1993). These similarities imply that novelty and positive affect may share, at least in part, common underlying mechanisms. In fact, a mechanism that has already been suggested to play a role in the influence of mild positive affect on cognition is release of dopamine into frontal brain regions and that process is also being suggested as important in the influence of novelty on cognition. Future research could investigate potential overlaps and differences in the effects of positive affect and novelty on cognition and behavior.

The present research makes several theoretical contributions. It extends the existing literature on novelty by demonstrating that novelty produces contextual effects that extend beyond the novel items themselves. While a significant body of research has examined how the degree of novelty of an item influences processing, preferences, or choice of that item (e.g., Anand and Sternthal 1990; Berlyne 1960; Steenkamp and Gielens 2003), the downstream effects of novelty exposure on subsequent preferences and choice have received little attention. This manuscript is the first to demonstrate that the ability of novelty to promote exploration applies not only to the novel items themselves, but also to items encountered in a follow-up context.

The present manuscript contributes also to the literature on variety seeking and innovation at the individual consumer level. A significant portion of the work in these areas has focused on the role of demographic and personality variables that determine one's propensity to seek variety or innovate, and on designing appropriate scales to measure these variables (e.g., Baumgartner and Steenkamp 1996; Raju 1980; Steenkamp and Baumgartner 1992). Less has been done to investigate the influence of variables that are under the direct control of marketers (e.g., Barone et al. 2000; Kahn and Isen 1993). The present paper begins investigation of the effects of one such variable, exposure to novelty, on varied and innovative consumer behavior.

Finally, by bringing together findings from several different literatures, the present research demonstrates how findings at the neurological level of analysis can be used to make predictions about effects that can be tested using traditional measures. It also suggests potential avenues for future research on the effects of exposure to novelty - a topic that is understudied in the consumer behavior literature, but that is of clear importance in this domain.

It is obvious from observing marketing practice that novelty is of central concern to managers: firms constantly tout newness and novelty, from claims of "new," to frequent changes in store displays, novel product introductions, and innovative advertising campaigns. The present work helps to illuminate why marketers place such emphasis on novelty: it has powerful effects on product choice and evaluations. The present studies suggest that when a firm introduces novelty, this may affect not only preference and choice of the novel product lines, packaging, brochures, etc, but also preferences, choice, and sales of existing products. Specifically, novel introductions may prompt consumers to seek diversity and try a broader range of product options. This should benefit a firm that already has varied product lines, since novelty will likely stimulate trial and purchase of more of its existing product options.

The results from our studies also suggest that a novel context such as a novel website of an online retailer, or novel décor or layout of a traditional retailer, may make consumers more open to, and may thus facilitate, trial and adoption of both new and not-so-new products. If a firm's existing product lines, however, are limited, novelty may decrease loyalty and prompt consumers to try competitors' products. Thus, this work suggests that firms should extend their product lines, in order to give customers the opportunity to obtain variety within the brand, especially if the firm's products feature newness. These, and many other questions, remain to be explored.

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CHAPTER 2

EVIDENCE FOR REWARD CIRCUITS IN THE BRAIN

Most animals and humans have a propensity to seek out and approach objects or events that have appetitive (rewarding) value and to avoid those that have aversive (punishing) value. Psychologists have long recognized the existence of these action or motivational tendencies and have attributed them to the functioning of two distinct systems for the regulation of human behavior. One system is involved in appetitive motivation and approach behavior and has been termed a behavioral approach system (e.g., Gray 1990). A second system deals with aversive motivation and avoidance behavior, and is mostly known as a behavioral inhibition system (Gray 1990). The approach and inhibition systems are believed to have partially distinct neural substrates and to exert distinct influences on behavior (Carver 2006).

The concept of "reward" is central to understanding the approach system and appetitive behavior. Some researchers have proposed that reward is not a unitary concept and that rewards involve functionally distinct components. For example, Schultz (1998) has suggested that one function of rewards is to induce subjective feelings of pleasure and positive affective states, a second function is to increase the frequency and intensity of behavior leading to such objects (learning), and a third function is to elicit approach and consummatory behavior. Similarly, Berridge and Robinson (2003) have proposed that rewards are associated with functionally separate feeling (what they call "liking"), learning, and motivational ("wanting") components. While there may be no final agreement over the exact components of rewards, it may be useful to keep the above described distinctions in mind since they are reflected in the literature on the brain mechanisms of reward. For example, theories about the

functions of the neurotransmitter dopamine have linked it to different aspects of rewards: some have implicated dopamine in the pleasant feelings accompanying reward (e.g., Wise 1980, 1982), others have argued for a role of dopamine in learning (e.g., Schultz 1998), and others – for a role of dopamine in motivated behavior (e.g., Berridge and Robinson 1998). Research exploring the exact mechanisms through which dopamine mediates reward processing is still ongoing. The present paper reviews some of the more prominent theories about the role of dopamine in reward processing. We also review evidence for the involvement of other brain areas and circuits in reward processing and outline some of the related controversies and outstanding issues.

Neural Representations of Reward: Evidence for the Role of Dopamine

The neurotransmitter dopamine (DA) has long been implicated in mediating the rewarding effects of natural stimuli. DA neurons are located mostly in the substantia nigra (SN) and the medially adjoining midbrain ventral tegmental area (VTA), in groups numbered A8 to A10. The *nigrostriatal dopamine system* consists of DA-producing cells in the SN pars compacta that project into the dorsal striatum (the input structure of the basal ganglia that consists of the caudate nucleus and putamen). This system is considered crucial for the regulation of motor functions, although evidence suggests its possible implication in cognitive functions such as learning (Kimura and Matsumoto 1997). The *mesocorticolimbic dopamine system* consists of DA-producing cells in the VTA that project to cortical and limbic areas such as the prefrontal cortex, the anterior cingulate, the ventral striatum (with the nucleus accumbens), the amygdala, the hippocampus, the olfactory bulb and cortex, and locus ceruleus. This system has been primarily associated with reward and motivation.

Several lines of evidence have implicated DA neurons, in particular those in the VTA, as well as neurons in DA-receiving structures such as nucleus accumbens and the prefrontal cortex (in particular the orbitofrontal cortex) in reward processing. First, drugs of abuse such as morphine, cocaine, or amphetamines influence DA neurotransmission by increasing DA concentration in the ventral striatum and frontal cortex, which appears to be a critical mechanism of drug addiction (Wise 1996a; Wise 1996b). Conversely, DA antagonists (e.g., neuroleptics) attenuate the rewarding effects of food and other reinforcers (Wise 1982). Second, studies of electrical self-stimulation reveal that many of the stimulation sites are in close proximity to axons of DA neurons or to axons presynaptic to them and intra-nucleus accumbens injections of DA antagonists disrupt self-stimulation behavior (see Ikemoto and Panksepp 1999 for a review). Furthermore, studies investigating the neuronal mechanisms of reward by observing the impulse activity of single DA neurons in the VTA show that DA neurons are activated by the rewarding characteristics of a wide range of somatosensory, visual, and auditory stimuli (Schultz 1998). About 75% of DA neurons show phasic activations following primary food and liquid rewards and a slightly smaller percentage of the DA population (55 - 70%) responds also to conditioned, reward-predicting stimuli (Schultz 1998). Only 11-14% of DA neurons show activations following primary aversive stimuli (e.g. air puff, electric shock, or tail pinch) or conditioned aversive visual or auditory stimuli (Mirenowicz and Schultz 1996; Schultz and Romo 1987), suggesting that the phasic responses of neurons "preferentially report environmental stimuli with appetitive value" (Schultz 1998). Neurons in the dorsal and ventral striatum, structures that receive dense DA projections from the SN and VTA respectively, have also been shown to increase activity in anticipation of as well as following reward delivery (Schultz et al. 1992). Finally, indirect evidence for the involvement of DA in reward processing comes from

a number of neuroimaging studies with humans that show activations in brain regions that receive direct VTA DA projections such as the nucleus accumbens, the amygdala, the orbitorfrontal cortex, and the anterior cingulate cortex, in anticipation of or during exposure to a wide range of rewarding stimuli (e.g., Aharon et al. 2001; Blood et al. 1999; Breiter et al. 2001; Menon and Levin 2005; Mobbs et al. 2003) or during reward-related decision making tasks (Bush et al. 2002).

The exact role of DA in reward-processing has been the subject of heated discussions (see Berridge 2007; Salamone 2007). Different theories have been proposed and while there seems to be more agreement now over some issues (e.g., that DA probably is not directly involved in the pleasant feelings associated with reward) still a lot of questions remain open. In this paper we review some of the more prominent hypothesis for the role DA in reward mechanisms.

The Role of Dopamine in the Pleasure Component of Reward Processing

Arguments Supporting the Anhedonia Hypothesis. Early theories implicated the neurotransmitter DA as the primary neural substrate of pleasure or hedonia (Wise 1980; 1982). Most prominent among these theories was the so called "anhedonia hypothesis" proposed by Roy Wise (Wise 1980; 1982). In the earlier and stronger version of this hypothesis, it was suggested that "the dopamine junctions represent a synaptic way station… where sensory inputs are translated into the hedonic messages we experience as pleasure, euphoria or 'yumminess'" (Wise 1980, p. 94). Later, however, Wise and his colleagues revised their position to say that the blockade of DA attenuates above all the motivational impact of positive reinforcers and that the evidence suggesting that neuroleptics disrupt the subjective hedonic effects of rewarding stimuli is mixed (Wise 1985).

The DA theory of positive affect advanced by Ashby, Isen and Turken (1999) proposes that positive affect is associated with increased brain levels of DA, but does not assume that the release of DA induces the pleasant feelings that accompany the experience of positive affect. Rather, the authors suggest, DA mediates some of the cognitive effects that have been observed with positive affect such as enhanced cognitive flexibility and facilitated creative problem solving through its influence on target sites such as the prefrontal cortex and the anterior cingulate.

The theory that argues most strongly against DA's role in mediating pleasure and positive affect is the incentive salience theory proposed by Kent Berridge and his colleagues (Berridge and Robinson 1998; Robinson and Berridge 1993). The incentive salience theory makes a distinction between the hedonic (what they call "liking") impact of rewards and their motivational (or "wanting") aspects and claims that DA mediates the motivational "wanting" component but not the pleasure-related "liking" component of rewards.

What is some of the evidence that has been brought against a causal role of DA in reward-related pleasure?

Arguments against the Anhedonia Hypothesis. A number of arguments have been brought against the hypothesis that DA is directly involved in the pleasant feelings associated with rewards. A prominent line of argumentation comes from Kent Berridge and his colleagues. They reported data showing that fundamental reactions to sucrose (tongue protrusions, licking) or bitter tastes (gapes) are not affected by dopaminergic lesions or by neuroleptic drugs (Berridge, Venier, and Robinson 1989). Even massive lesions that eliminate nearly all DA in the NAc and striatum of experimental rats fail to disrupt expressions of taste "liking" although they attenuate the animal's motivation to work for obtaining the sweet reward ("wanting") (Berridge and Robinson 1998). Conversely, increases in extracellular DA in mutant mice do not

increase hedonic "liking" reactions to sucrose (Pecina et al. 2003). Berridge and colleagues have argued that facial reactions to natural rewards such as sucrose are homologous across rodents, primates, and human infants and represent objective indicators of the hedonic impact of these rewards. Failure of DA manipulations to affect these expressions, therefore, is interpreted as evidence against DA's involvement in the pleasure aspect of rewards. Other researchers, however, have pointed out that the facial expressions observed in infants and rats in response to sweet taste may be related to stereotyped fixed action patterns of ingestion rather than to forebrain mechanisms of motivation and emotion (Wise 2004). Furthermore, the fact that increases in extracellular DA fail to increase "liking" reactions cannot be interpreted unequivocally, since there may be a ceiling effect and furthermore it is not clear that the relationship between DA levels and reward is a linear one.

A more convincing line of argumentation against DA's mediating role in reward-related pleasure comes from electrophysiological studies with animals by Schultz and colleagues (e. g., Schultz, Dayan, and Montague 1997) which show that DA neurons fire in response to rewards only during the first few presentations of the reward, while the reward is not fully predicted. Over the course of learning, the DA response gradually shifts towards the earliest conditioned stimulus predicting the reward and no firing at all is observed at the time of receipt of a reward that has been fully learned. This pattern of activation suggests that the DA response tracks a component of reward other than pleasure, since the pleasure impact should not completely disappear with learning.

Furthermore, DA neurons have been observed to respond strongly to intrinsically neutral novel stimuli and salient attention-grabbing stimuli such as loud clicks or large pictures (Ljungberg, Apicella, and Schultz 1992). A certain percentage of DA neurons respond also to conditioned aversive visual or auditory stimuli in

active avoidance tasks in which animals release a key to avoid an air puff or a drop of hypertonic saline (Mirenowicz and Shultz 1996). It is possible that both of these types of DA activation are reward related. For example, novelty itself may have reward value or may be potentially rewarding, in the sense that it motivates exploration in the search for potential reinforcers (Bunzeck and Duzel 2006). This latter possibility is supported by the observation that novelty responses decay gradually with repeated exposure but increase again if the stimulus is appetitively conditioned and subside rapidly if the stimulus is used for conditioning active avoidance behavior (Schultz 1998). There is no consensus regarding DA reactions to aversive stimuli in active avoidance tasks, however it seems possible that DA neurons may be responding to the rewarding aspect of relief from the aversive stimuli. Whatever the explanation for the novelty and the aversive DA responses, it is clear that these responses reflect an aspect of reward that is not pleasure related.

Another line of argumentation against the mediating role of DA in pleasure comes from the observation that there is rapid within-session tolerance to the subjective pleasure of rewarding drugs like cocaine, morphine, and nicotine, but there is little or no decrease in the ability of these drugs to sustain repeated and regular self-administration (Wize 2004). Finally, low doses of cocaine can control behavior even when they are subjectively indistinguishable from placebo (Martinez et al. 2004) and brain imaging studies have indicated that stimulant-induced euphoria is only loosely correlated with the degree of drug-induced DA release (Volkow 1999).

Thus there seems to be a growing body of evidence suggesting that DA maybe neither necessary nor sufficient to cause the sensory pleasure and the positive feelings associated with rewards. This component of rewards must then be mediated by a different neural substrate. What are some possible candidates that have been proposed?

Alternative Hypotheses. Researchers have suggested that the pleasant feelings associated with rewards may be mediated by forebrain opioid circuits involving structures such as the nucleus accumbens (NAc) and the ventral pallidum, and possibly the orbitofrontal cortex. NAc and the ventral palidum, located within the ventral forebrain and sharing reciprocal projections with one another, are considered to be part of the brain opioid system (Pecina, Smith, and Berridge 2006). Berridge and colleagues (Pecina and Berridge 2005; Smith and Berridge 2005) have suggested that each of these structures contains an anatomical subregion, a "hedonic hot spot" in which opioids amplify significantly the hedonic impact of sensory pleasure. In particular, Pecina and Berridge (2005) report that they have identified a 1-mm^3 – site within the medial shell subregion of NAc where a microinjection of the μ-opioid agonist DAMGO caused sucrose taste infusions into the rat's mouth to elicit up to quadruple the usual number of positive "liking" reactions such as licking and tongue protrusion. DAMGO injections in other areas of NAc stimulated a "wanting" for food as reflected in increased food intake, but did not increase "liking" reactions. Pecina and Berridge (2005) concluded that this particular "hot spot" in NAc possesses the ability to enhance positive hedonic impact. Another region that has been suggested as a likely candidate for a "hedonic hot spot" is in the caudal portion of the ventral pallidum – a region that is the chief output target of the NAc projections (Pecina et al. 2006). The features of this area are similar to those of NAc. Microinjections of the μ-opioid agonist DAMGO in the ventral pallidum of rats were also found to double the number of hedonic "liking" reactions to a sucrose taste (Smith and Berridge 2005). Smith and Berridge (2007) recently reported that they observed significant interaction between NAc and ventral pallidum activation in rats, in the sense that activation of one area recruited activation in the other and the two areas were needed together to

enhance sucrose "liking" reactions, essentially cooperating within a single NAc-ventral pallidum circuit.

The above described evidence for the existence of “hedonic hot spots” in the NAc and the ventral pallidum is still preliminary. First, it comes only from rodents and it is not clear that similar effects will be observed with human subjects. Second, it is not clear how exactly the proposed areas amplify the observed reward-related experiences of pleasure. Berridge and his colleagues have suggested that it may be through the increased density of μ-opioid receptors in these regions, but the exact mechanism is not clear. Third, the interpretation of the evidence is based on the assumption that facial reactions to sweet tastes represent an objective measure of hedonic impact. As pointed out earlier, it is quite possible that such expressions are in fact fixed action patterns of ingestion. Further research is needed to clarify the role of the above described regions in mediating pleasure and also to explore the role of forebrain opioid circuits in this process.

In summary, there seems to be a growing consensus among researchers that DA does not mediate the hedonic component of rewards. Forebrain opioids have been proposed as a possible alternative, and it has been suggested that brain areas rich in opioid receptors form networks that coordinate multiple such hedonic “hotspots.” Further research is needed to identify likely members of these networks and to clarify the underlying mechanisms, including other possible neurotransmitters, through which such regions may cause or amplify the hedonic impact of rewards.

The Role of Dopamine in the Learning Component of Reward Processing

Arguments supporting a role of dopamine in learning. The value of some rewards (primary, or unconditioned rewards) may be determined by innate instincts and support initial approach behavior and ingestion in early life. These include, for

example, the preference for an optimal temperature range, the preference for sweet and the rejection of bitter substances. The majority of rewards, however, acquire their appetitive value through associative learning during the life experience of the organism. Associative appetitive learning involves basic Pavlovian stimulus-stimulus (S-S) or stimulus – response (S-R) conditioning, or instrumental conditioning (response-contingent reinforcement). In Pavlovian conditioning, a neutral stimulus (the conditioned stimulus, CS) is presented repeatedly along with a primary unconditioned reward (UCS). With time, the CS starts eliciting conditioned responses (CRs) which can be anticipatory responses, behavioral habits, or even conditioned motivations and emotions appropriate to the UCS. In instrumental conditioning, the behavioral response itself becomes associated with the reward and obtains appetitive value. Thus in the instrumental form of incentive learning, rewards become "incentives" and serve as goals of behavior following associations between behavioral responses and outcome – the common notion of rewards being obtained for having done something well. Higher forms of learning, of course, are more elaborate and involve multiple relationships among stimuli and actions, including representations of temporal, spatial, predictive and causal relationships that guide goal-directed plans of action.

Associative learning depends on the discrepancy between the occurrence of a reward and its prediction. The importance of such prediction errors is derived from Kamin's blocking effect (1969) which postulates that a reward that is fully predicted does not contribute to the learning of a stimulus or action, even when it has been repeatedly paired with the stimulus or action. This is conceptualized in the associative Rescorla-Wagner learning rules (Rescorla & Wagner 1972), according to which learning advances only to the extent to which a reinforcer is unpredicted and slows down progressively as the reinforcer becomes more predicted. The omission of a

predicted reinforcer reduces the strength of the CS and produces extinction of behavior.

Data from a series of electrophysiological studies examining the relationship between phasic activation of DA neurons and the presentation of rewards and reward-predicting stimuli suggests that the DA system maybe well-suited to mediate reward learning, and in particular prediction-error based learning (Ljungberg, Apicella, and Schultz 1991, 1992; Mirenowicz and Schultz 1994, 1996).

The characteristics of the phasic DA response to reward-related stimuli are best illustrated in learning episodes during which rewards are important for acquiring behavioral responses. The DA reward signal has been shown to undergo systematic changes during the progress of learning (Ljungberg et al. 1992; Mirenowicz and Schultz 1994). Primary rewards elicit neuronal activations during initial learning periods which decrease gradually and are transferred to the conditioned, reward-predicting stimulus. If a predicted reward fails to occur, DA neurons are depressed at the time the reward would have occurred. With increased learning, activation transfers from the primary reward to the earliest conditioned stimulus. Subsequently appearing conditioned stimuli and primary rewards activate DA neurons only transiently while they are uncertain and new contingencies are being established (Schultz 1998). Thus reward unpredictability is a crucial feature of the phasic DA response. This feature has been termed "reward-prediction error" (Schultz et al. 1995, 1997) and has been formalized as follows:

Dopamine Response (Reward) = Reward Occurred – Reward Predicted.

The criterion of unpredictability includes the time of reward, as well as the magnitude of the reward. Specifically, Hollerman and Schultz (1998) demonstrated that rewards elicit transient activations when they are delivered earlier or later than predicted (Hollerman and Schultz 1998). Tobler, Fiorillo, and Schultz (2005) showed

that DA neurons process also received-reward magnitude relative to a predicted magnitude. For example, in one of their experiments, macaque monkeys learned the association between neutral stimuli and the probability of delivery of liquid reward (fruit juice) in three possible volumes: small, medium, and large. One stimulus predicted that either the small or the medium volume of juice would be delivered with equal probability, whereas another stimulus predicted either the medium or the large volume with equal probability. In both cases, delivery of the larger of the two potential volumes elicited an increase in DA activity, whereas the smaller volume elicited a decrease. Thus a reward outcome that is positive on an absolute value scale can nonetheless suppress the activity of DA neurons.

Schultz (2002) has suggested that the phasic DA reward-predicting signal exerts an enhancing and focusing effect in other cortical structures such as the striatum and the prefrontal cortex by increasing the signal-to-noise ratio of active inputs to neurons in these structures. In particular, the DA signal presumably modifies the ways in which other simultaneous inputs influence post-synaptic neurons, by prioritizing reward-related inputs over other inputs. As a consequence, the phasic DA signal is proposed to produce a rapid switch of attentional and behavioral processing to reward-predicting events that may lead to Hebbian-type plasticity at synapses in the stratum and cortex and thus may facilitate long-term potentiation. A similar view of DA's role in reward learning has also been expressed by Cohen, Braver, and Brown (2002) who suggest that the phasic DA signal has two functions in the prefrontal cortex: an updating function and a reinforcement learning function. In their updating function, phasic bursts of DA activity function as a "gating mechanism" by signaling when input should be selected and stored in the PFC, updating the contents of working memory to convey important reward-related information. This occurs through the transient potentiation of both excitatory afferent and local inhibitory effects in the

PFC. The learning effect occurs through modulation of synaptic weights, driven by the error-prediction signal carried by phasic DA release.

Arguments against dopamine's role in reward learning. Some researchers have expressed skepticism regarding the causal role of DA in reward learning (Berridge 2007). While admitting that DA makes "many indirect contributions to both learning and learned performance" Berridge and colleagues have questioned whether "dopamine activation causes the rest of the brain to learn, or instead, whether learning by other brain systems causes dopamine activation" (Berridge 2007, p. 399). The alternative view they propose is that DA activation is an "output consequence of learning mechanisms operating elsewhere, rather than a causal mechanism for learning" (Berridge 2007, p. 399). The argument put forth by these authors against DA's mediating role in learning is based on data from experiments with rodents with depleted DA or with genetic inability to produce DA who still exhibit the ability to learn a reward preference (Berridge and Robinson 1998; Cannon and Palmiter 2003). For example, rats with 99% of their nucleus accumbens and the striatum DA depleted reportedly were still able to acquire and express an associative shift from hedonic reactions to aversion towards a stimulus that was originally paired with a reward (saccharine solution) but was subsequently paired with illness (Berridge and Robinson 1998). Similarly, Cannon and Palmiter (2003) report that mutant mice with a genetic inability to produce DA were still able to learn a preference for a spout that delivered sucrose solution over one that delivered water, even though they had virtually no DA in their brains. When the DA deficient (DD) mice drank, they drank more sucrose, and this preference was proportionally equal to that of control mice. However, the strength of these results is undermined by the fact that they were obtained after excluding 4 (out of 12 total) DD mice who actually did not drink at all, and the remaining 8 mice drank during only 1.6 out of the 4 tests. Furthermore, as pointed out by Ikemoto and

Panksepp (1999), conditioned taste preference/aversion is only one of many examples of Pavlovian conditioning, therefore these results should not be taken as proof that DA is not involved in other types of learning. In another recent paper, Cagniard and colleagues (Cagniard et al. 2006) also argue against DA's causal role in reward learning, basing their argument on evidence that increases in DA neurotransmission fail to cause better or faster learning about rewards. Specifically, in their studies DAT-knockdown mutant mice that had elevated extracellular DA levels of 170% above control mice failed to learn a Pavlovian conditioned approach association to a food dish faster than control mice, nor did they learn to bar press for food reward in an instrumental task any more quickly than wild-type mice. These results, however, should be interpreted with caution as it is not clear that the relationship between DA levels and learning is a linear one. It may well be that some intermediate level of DA (neither too low nor too high) is optimal for the facilitation of reward-related learning. In fact, it has been previously suggested that the effects of DA modulation on performance are non-monotonic: both too little and too much DA impair working memory performance (Cohen, Braver, and Brown 2002; Williams and Goldman-Rakic 1995), and phasic DA effects may further be dependent on tonic baseline levels of DA activation (Cohen, Braver, and Brown 2002).

Thus although some researchers have challenged DA's role in reward learning, the majority of evidence still points to a key role of DA in these processes. If the DA signal is not a direct cause of learning but rather a consequence of learning, as suggested by Berridge (2007), it is not clear where else in the brain reward learning first originates. In fact, characteristics of the phasic dopamine signal, with its sensitivity to differences in expected and obtained reward make it the most plausible candidate for explaining learning without the danger of introducing regress in the process.

The Role of Dopamine in the Motivational Component of Reward Processing

Several lines of evidence suggest that DA mediates the motivational component of rewards and that it is through DA signaling that a neutral stimulus is converted into an attractive one capable of eliciting approach behavior. For example, manipulations of DA and related mesolimbic circuits in animals induce powerful changes in the observed instrumental performance of these animals for food, drugs, and electrical brain stimulation (Salamone 1994; Wise 1982; 1985). Specifically, Salamone and colleagues demonstrated that rats with 6-OHDA-induced DA depletion of the NAc forgo the opportunity to press a lever for preferred food, instead consuming more of a less preferred but freely available food (Salamone et al. 1994). It is now generally accepted that the changes in approach behavior elicited by suppression of DA neurotransmission reflect motivational and not simply motor deficits (Robinson and Berridge 1993). Rats with extensive destruction of the DA system starve to death unless nourished artificially, even though food is readily available and even though they retain the motor capacity to walk, chew, swallow, and perform other movements necessary for eating (Berridge, Venier, and Robinson 1989). Conversely, administering amphetamine injections directly into the NAc of rats causes increases in "wanting" for sucrose reward as measured by the rate of lever pressing to obtain the reward (Wyvell and Berridge 2000). Indirect facilitation of DA neurotransmission by electrical brain stimulation also increases the seeking behavior and the actual ingestion of palatable food, even though there is no increase in the hedonic impact of food as measured by changes in facial reactions to the food (Wyvell and Berridge 2000).

Based on the above evidence, Berridge and colleagues have proposed that dopamine mediates the motivational component of rewards - an idea captured in the

incentive salience hypothesis of DA function (Berridge and Robinson 1998; Robinson and Berridge 2003). Incentive salience is defined as the process through which sensory information about rewards and their cues are transformed into "attractive, desired, and riveting incentives" (Berridge and Robinson 2003, p. 510) and through which stimuli become "wanted" and able to elicit voluntary action. Incentive salience or "wanting," as defined by Berridge and Robinson (1998), is separate from hedonic "liking" or sensory pleasure, and is also separate from learning, although "it takes all three types of components coordination together to produce the full phenomenon we usually think of as reward" (Berridge 2007, p. 408). The hypothesis proposes that the DA system is necessary for the attribution of incentive salience to stimuli, but not for hedonic activation or for the learning of reward-related associations.

Berridge and Robinson's arguments are based primarily on evidence that dopaminergic deficits impair the instrumental behavior of animals for rewards but do not impair taste reactivity reactions. Some authors, however (Ikemoto and Panksepp 1999; Wise 2004), have pointed out that if it is only the motivational component of reward that is compromised under neuroleptics or other forms of dopamine impairment, then responding to rewards should not be normal from the very beginning of neuroleptic treatment. Studies however show that neuroleptic-treated animals usually continue to approach rewards and reward-predicting stimuli until they have had a considerable experience with the reward under the influence of the neuroleptic (Wise 1982). Wise argues that the fact that responding decreases gradually and only after an initial experience with the reward under the neuroleptic influence suggests that it is more than just the motivational component that is being affected (Ikemoto and Panskepp 1999; Wise 2004). Thus it is not clear that a clean distinction between the motivational and the other functions of dopamine in reward processing is feasible.

It may be rather that dopamine functions in a more complex way affecting different reward-related processes simultaneously.

Some researchers have suggested that all stimuli that are salient or have motivational significance, and not only those with rewarding properties, activate DA neurons (Redgrave, Prescott, and Gurney 1999). For example, as mentioned before, physically salient sensory stimuli such as tones and lights have been shown to evoke rapid, phasic excitations in DA neurons (Ljungberg, Apicella, and Schultz 1992). Also, novel stimuli of neutral valence can also evoke DA release (Schultz 1998). However, if DA activations coded all salient and motivationally relevant events, then we should not observe depression of DA activation following the omission of a predicted reward which in itself represents a salient event with motivational consequences. Furthermore, some researchers have suggested that DA release to novel stimuli may reflect the fact that novelty can be rewarding (Kakade and Dayan 2002) which is consistent with research in social psychology suggesting that moderate novelty can be rewarding (Berlyne 1970).

Dopamine: Outstanding Issues

While each of the above described theories of DA highlights a certain aspect of its role in reward processing, none of these theories can comprehensively account for all of DA's functions. Many issues still remain to be clarified. One issue we haven't mentioned so far concerns the distinction between phasic and tonic DA signals, and their respective function. In addition to the fast and short-lasting phasic dopaminergic activations that have been the target of investigation in most electrophysiological studies of DA function, DA neurons exhibit also sustained tonic activations. There is no clear agreement on the definition and functions of tonic DA response. Grace (1991) defines phasic DA release as the quick (within milliseconds) release of DA from axon

terminals into the synaptic cleft in response to action potentials, and tonic DA release as the extrasynaptic concentration of DA that is independent of phasic activations and occurs much slower, over period of tens of minutes to hours or days. It has been suggested that tonic DA levels modulate the phasic DA response (Grace 1991). Studies by Lisman and Grace (2005) suggest that novelty-related increases in tonic DA inputs in the hippocampus facilitate long-term potentiation (LTP) and memory encoding. Yet others have proposed that tonic changes in DA levels may play a critical role in motivation and affect (Ikemoto 2007). The current literature does not offer sufficient information on the functional relation between tonic and phasic DA or on the possible role of tonic DA for reward processing.

To complicate things even further, recent work by Tobler et al. (2005) suggests the existence of yet a third type of DA response – an "intermediate" response which occurs in the time between the onset of a conditioned stimulus and the delivery (or omission) of a reward. Electrophysiological responses of single midbrain DA neurons were recorded from adult macaca monkeys who were trained in a classical conditioning procedure to respond to conditioned stimuli associated with distinct reward probabilities (0.0, .25, .50, .75, or 1.0). A sustained activation of DA neurons was recorded that seemed to be independent of the phasic DA response. This slower response was highest when the probability of reward was 0.5 and was minimal at the two endpoints of probability (0 or 1). It occurred only for motivationally relevant stimuli: no sustained activation was observed when the animal was exposed to probability/uncertainty patterns for reward-unrelated stimuli. Furthermore, the magnitude of the sustained response seemed to be proportional to the discrepancy between potential rewards: it was strongest after a stimulus predicting either a small or a large reward (a large discrepancy), and was significantly weaker for smaller discrepancy combinations (small – medium, and medium – large). Tobler and his

colleagues suggested that these results have significant implications for understanding the psychological mechanisms of gambling: the allure of gambling may well come partially from the uncertainty of the gains. Just as the monkey neurons in the experiment responded most strongly to the most discrepant potential rewards, so in gambling one may be drawn in by the extreme prospects of a loss or a jackpot. The relation of the response to predicted reward discrepancy may also have important implications for learning. Tobler et al. (2005) hypothesize that the sustained activation of DA neurons may play a role in mobilizing attention and facilitating learning. The organism has the most to learn when uncertainty is highest – hence the peak response at P = .5. Along the same lines, one could say that the organism has more to learn the wider the range of potential outcomes. It would be important for the organism to figure out the pattern of a stimulus that can predict both a very small and a very large reward. Thus a situation characterized by the highest degree of uncertainty: probability of reward = .5 coupled with the widest range of potential reward outcomes, should induce the largest amount of sustained DA activation. It would be interesting to test these ideas in a decision-making study with human participants.

Neural Representations of Rewards: Evidence for the Existence of Reward Circuits

Types of Reward Circuits and Their Components

So far we have reviewed evidence for the direct involvement of DA neurons in reward processing. As mentioned earlier, however, DA neurons in the VTA project to a number of brain structures among which the NAc, the orbitofrontal cortex (OFC), the amygdala, the anterior cingulate cortex (ACC), the hippocampus, and the olfactory tubercle. Evidence suggests that these structures are also involved in reward

processing and that, together with VTA DA neurons, they form neural circuits for reward.

The mesolimbic dopamine system involves dopamine projects from the VTA to structures considered part of the limbic system such as the NAc, the amygdala, the hippocampus, and the olfactory tubercle. This system is considered to be involved in reward processing.

Many lines of evidence suggest that the *nucleus accumbens* plays an important role in mediating reward effects. For example, animals self-administer DA agonists or drugs that increase DA levels like amphetamines directly into the NAc; given a choice between environments where animals previously received microinjections of DA agonists (vs. vehicle) into the NAc, animals spend more time in the drug-paired environments; intra-NAc injections of amphetamines facilitate self-stimulation behavior, while administration of DA antagonists disrupts such behavior and these effects are not simply due to motoric effects of self-stimulation; DA depletion by lesions in the NAc abolishes or severly disrupts intravenous self-administration of psychostimulant drugs (see Ikemoto and Panksepp 1999 for a comprehensive review). Furthermore, single-neuron studies with monkeys have shown that NAc neurons are activated during the expectation of primary rewards (Schultz et al. 1992). Bardo et al. (1996) suggested that NAc is involved in novelty-seeking behavior, in anticipation of possible rewards. When NAc-DA depleted rats and control rats are tested in an environment with salient stimuli (novel stimuli and incentive stimuli), the control animals exhibit heightened locomotor activity toward the salient stimulus, while NAs-DA depleted animals do not readily respond to such stimuli, although they do not exhibit general locomotor deficits. The authors suggest that these results imply a failure on the part of the NAc-DA deficient animals to initiate approach and exploratory responses in the presence of salient environmental stimuli. A similar view

is expressed by Ikemoto and Panksepp (1999) who have suggested that the primary role of NAc DA is to respond to novelty and to "focus the sensorimotor apparatus into approach, seeking, and investigatory activities directed toward novel events, especially if they are related to rewards (Ikemoto and Panksepp 1999, p. 33).

The role of the *amygdala* in processing reward is not clear. This structure has traditionally been implicated in the processing of negative, unpleasant emotions such as fear and in associating environmental stimuli with emotionally charged, aversive sensory outputs (Baxter and Murray 2002). Recently, claims have been made for a role of the amygdala in the processing of pleasant stimuli. For example, O'Doherty et al. (2001) reported fMRI evidence suggesting that the human amygdala is activated by pleasant as well as aversive tastes. In five out of seven subjects, the amygdala was activated by the pleasant taste of glucose, and four out of seven showed activations by the aversive taste of salt. Also, Rolls et al. (2003) reported that activation by pleasant touch was produced in an area in or near the amygdala. Still, the majority of studies have failed to observe increases in amygdala activation to the presentation of rewarding positive stimuli. However, there is now considerable experimental evidence that the amygdala has a role in a specific kind of stimulus-reward learning (Baxter and Murray 2002). Specifically, the amygdala does not seem to be important for classical Pavlovian S-S or S-R learning, or for instrumental learning. Complete removal of the amygdala in rats does not disrupt these types of learning. What does get disrupted with damage to the amygdala is the learning of current stimulus-value associations (Baxter and Murray 2002; Hatfield et al. 1996). Current stimulus-value associations require the acquisition and rapid updating of a representation of reinforcer value, and the linking of this to object representation. One type of stimulus-value association is exemplified in the so-called reinforcer-devaluation experimental paradigm. In this paradigm, behavioral performance depends on the capacity of the stimulus to evoke a

representation of the current value of the reinforcer. For instance, pairing the ingestion of a food reinforcer with illness (induced by injections of lithium chloride) in rats substantially reduces subsequent responding to a conditioned stimulus that has been paired with that food. This effect has been shown to be completely abolished by neurotoxic lesions of the basolateral amygdala (Hatfield et al. 1996). This implies that, following lesions to the amygdala, either the stored information about reward value cannot be updated, or else any successfully update information about reward value cannot affect response selection (Baxter and Murray 2002).

The *hippocampus* is believed to be involved in the formation of episodic memories and in spatial navigation. Evidence about the involvement of the hippocampus in reward processing is insufficient. Recent studies by Rolls and Xiang (2005) suggest that it may be involved in forming reward-place associations. In a reward-place association task, neurons in the hippocampus of monkeys responded preferentially to the location of a more (relative to a less) preferred reward, and reversed the location to which they responded after the locations of the preferred and less preferred rewards were switched. No such patterns of activation were observed in visual discrimination or object-association type of tasks. Thus there is some initial evidence that the hippocampus may facilitate the association of places with rewards available.

The mesocortical dopamine system consists of VTA dopamine projections to the prefrontal cortex and the anterior cingulate.

A region in the PFC that is often associated with reward is the *orbitofrontal cortex (OFC)*. Neurons in more caudal OFC regions process gustatory, olfactory, and somatosensory reward information. For example, OFC contains the so called "secondary taste cortex" in which taste is represented, as well as olfactory areas in which information about the identity and the reward value of odors is represented

(Rolls 2004). Furthermore, Rolls et al. (2003) used fMRI to compare activations produced by pleasant, painful, and neutral touch, to the left hand of human subjects. It was found that OFC regions were activated more by very light pleasant touch (soft velvet) and by painful touch (pointed stylus) than by more physically strong but affectively neutral touch (wooden dowel). The affectively neutral touch activated more areas of the somatosensory cortex. Evidence suggests that pleasant and unpleasant sensory stimuli may be represented in dissociable parts of the OFC. Fore example, Kringelbach, and de Araujo. (2003) reported that pleasant (floral, sweet, woody) odors activated a medial region of the OFC and that this activation was reliably correlated with subjective pleasantness ratings of the odors. Unpleasant odors, on the other hand (hexanoic acid, octanol) activated lateral parts of the OFC. Similarly, tastes that were subjectively rated by participants as pleasant (sweet taste) or aversive (salt taste) activated areas in the OFC that were adjacent but with little overlap (O'Doherty et al. 2001). The question arises whether it is the pure reward value, and not the sensory properties of taste and odor that are represented in OFC. Studies with animals show that the responses of orbitofrontal taste and odor neurons, unlike responses in the primary taste cortex, are modulated by hunger and satiety. For example, neurons in OFC of monkeys responded to a particular food taste or odor when an animal was hungry but decreased their firing rate once the animal was satiated and the corresponding food was no longer rewarding (Critchley and Rolls 1996). Similarly, in humans, OFC activation to food (chocolate milk or tomato juice) decreased after the food had been eaten to satiety (Kringelbach et al. 2003). Furthermore, Rolls (2004) reviewed neurophysiological, imaging, and lesion evidence indicating that OFC is involved in Pavlovian type association learning and in the correction of associations when reinforcement contingencies in the environment change. In one study, OFC visual cells in monkeys reliably discriminated between the sight of different geometric

shapes (e.g., triangle vs. square) when those shapes were differentially rewarded in the task (Rolls et al. 1996). Importantly, when the reward associations of the stimuli were reversed, this resulted in a rapid behavioral learning of the new reward associations and in a reversal in the responses in 70% of the OFC neurons to the visual stimuli. This evidence suggests that OFC may also be involved in reward-related learning.

Another structure in the mesocortical DA system that has been implicated in reward is *the anterior cingulate cortex (ACC).* The human ACC can be divided into two major subdivisions: a rostral-ventral affective division (aACC) and a dorsal cognitive division (dACC) (Bush, Luu and Posner 2000). The affective subdivision of ACC is connected to several structures among which the amygdala, NAc, OFC, and the hippocampus, and is believed to be involved in assessing the salience of emotional information and the regulation of emotional processes (Bush et al. 2000). The cognitive subdivision of the ACC has been ascribed a number of different functions, including attention-for-action/target selection, motivational valence assignment, motor response selection, error detection/performance monitoring, competition monitoring, anticipation, working memory, novelty detection, and reward assessment (see Bush et al. 2002). The wider range of cognitive functions in which the ACC has been implicated suggests that a unimodal theory of its function would not be appropriate.

Evidence from studies with both animals and humans implicates the dACC in reward processing. For example, Nishijo et al. (1997) reported data from single-unit recordings from the cingulate motor area in monkeys (CMAr, equivalent of the human dACC) indicating the existence of neurons that preferentially respond to rewards. For example, one group of neurons in the monkey CMAr responded exclusively to rewarding (cookie, apple) but not to aversive (syringe, brown cylinder associated with electric shock) or neutral (yellow cylinder with no association) stimuli, while a different group of CMAr neurons responded during bar pressing to obtain reward but

not during bar pressing to avoid shock. In humans, a study by Bush et al. (2002) found evidence for the existence of dACC neurons responding to reward-related stimuli. The study involved a reward-based decision-making task. Each trial of the study began with the display of an asterisk in the middle of the computer screen, and in response participants had to press one of two key buttons. The key presses were followed by one of three possible types of feedback. One feedback was "$$$$$" (CONrew) and it indicated that the participant had hit the correct button and would obtain 15c. Participants were instructed that if they got this feedback, they should continue pressing the same key until they received one of two other possible feedbacks: either a "$$$" (REDrew), indicating that they received a reduced reward of 9c. and should therefore switch to pressing the other button on subsequent trials to get the full reward, or "SWTCH", indicating that they should press the other button to receive the full reward of 15c. fMRI results showed that in 7 out of 8 participants, dACC activity was uniformly highest on the REDrew trials. Furthermore, dACC activity was significantly larger on REDrew and SWITCH trials relative to CONrew trials, and even more importantly, dACC activity on REDrew trials was significantly larger than dACC activity on SWITCH trials. These results indicate that dACC neurons responded specifically to reward-related feedback, and not to any non-specific act of switching/change behavior, providing support for the hypothesis that dACC is involved, among other things, in reward-based decision making.

Besides reward-based decision making, the dACC has also been implicated, as mentioned before, in working memory and in executive function tasks, and Ashby et al. (1999) have also provided extensive evidence that the dACC is involved in the selection of cognitive perspective – all functions assumed to be mediated by DA. If dACC's role in the reward-based decision study by Bush et al. (2002) is also mediated by DA, then it's not easy to explain why in this study dACC neurons were activated

following reduced reward, while DA activity generally is suppressed following the reduction or absence of rewards. Thus, as pointed out by Bush et al. (2002), the story about ACC's involvement in reward processing may not be simple. Further research is needed to clarify the exact role of dACC in reward processing.

Responses to Abstract Rewards – Evidence from fMRI Studies

Neuroimaging studies exploring responses in humans to rewards of more abstract nature such as music, humor, beauty, and wealth complement our understanding of the function of the mesolimbic and the mesocortical dopaminergic systems, sometimes referred collectively as the mesocorticolimbic dopaminergic system in reward processing and provide further evidence for the existence of reward circuits in the brain.

For example, Menon and Levitin (2005) examined brain responses to classical music using high-resolution fMRI. Results showed that listening to pleasant music significantly modulated activity in parts of the mesolimbic system such as the VTA and the NAc, as well as the hypothalamus which is known to regulate autonomic responses such as heart rate and respiration. Furthermore, responses in the NAc and the VTA were highly correlated suggesting an association between VTA DA release and NAc response. Another study on the rewarding effects of music examined cerebral bloodflow increases and decreases as a function of music consonance/dissonance (Blood et al. 1999). Activations were observed in areas such as the OFC, parahippocampal gyrus, and subcallosal cingulate that were highly correlated with subjective ratings of pleasantness and were also distinct from activations in areas involved in perceptual processes such as the secondary auditory cortex.

An fMRI study by Mobbs et al. (2003) demonstrated that humor also engages a network of subcortical structures including components of the mesolimbic

dopaminergic system such as the VTA and NAc, as well as the amygdala. Exposure to funny (vs. nonfunny) cartoons elicited reliable activation in these areas, and in particular in the NAc.

Aharon et al. (2001) investigated the rewarding effects of beauty on brain activity in areas implicated in reward processing. Young heterosexual males viewed photographs of beautiful and average female faces and beautiful and average male faces. Three types of measures were taken: self-reported ratings of face attractiveness, a behavioral measure that involved pressing a key to change the relative duration of viewing the different images, and fMRI measures of brain activation in response to the viewed faces. Results from the rating and the keypress tasks revealed dissociation between self-reported evaluations of attractiveness and quantified measures of reward valuation. In particular, male subjects rated beautiful male faces as very attractive but did not expend effort (as measured by keypresses) to increase the viewing times of these faces as they did for beautiful female faces. The fMRI data showed patterns of activation in areas of the mesolimbic dopaminergic system such as the NAc, the VTA and an area of the amygdala (the sublenticular extended amygdala) that correlated with keypresses but not with ratings. In particular, there were positive signal changes in these structures for male participants viewing the beautiful female faces versus average female faces and relative negative signal changes for beautiful male versus average male faces.

Using event-related fMRI, Knutson et al. (2001) investigated brain activation in response to the anticipation of increasing monetary rewards and punishments. While anticipation of both rewards and punishments increased activation in the medial caudate, only anticipation of increasing rewards was found to elicit significantly increased activation in the NAc that was also correlated with participants' self-reported happiness. Neural responses to the anticipation and experience of monetary

rewards and punishments were also investigated in an fMRI study by Breiter et al. (2001). Participants took part in a game of chance for which they were provided with a monetary endowment and informed that during the game they might lose some or all of this money, retain it or increase it. Each experimental trial consisted of a prospect (or expectancy) phase, and an outcome phase which made it possible to distinguish brain signals of anticipation from those associated with the actual monetary outcomes. Analysis of the imaging data revealed that the most sustained responses to prospects were observed in the sublenticular extended amygdala (SLEA) and the OFC. Reliable responses to the good spinners were also observed in the NAc and the hypothalamus, while the amygdala tracked the expected values of the bad spinner. Outcome responses were recorded in the NAc, the SLEA, the hypothalamus and the VTA, suggesting little segregation of prospect and outcome responses. Importantly, activations in DA terminal regions such as the NAc, SLEA, and hypothalamus showed impressive parallels to patterns of VTA DA neuron firings in monkeys during anticipation and experience of food or juice rewards. The researchers concluded that these parallels are "consistent with the involvement of common, generalized circuitry in the processing of different categories of rewards" (Breiter et al. 2001, p. 627).

Conclusion

Evidence from a wide range of electrophysiological, lesion, pharmacological, and imaging studies with both humans and animals suggests that the specific brain regions such as the dopaminergic midbrain, striatum, orbitofrontal cortex, anterior cingulate cortex, and the amygdala play a role in representing reward. These regions are highly interconnected and together can be considered as an integrated network for representing reward. Studies have tried to tease out the exact contribution of these

areas to reward processing, i.e., whether the area is involved in learning about rewards, in amplifying the pleasant feelings associated with rewards, or in mediating the instrumental value of rewards. Distinctions have also been made between responding to rewards vs. responding to the anticipation of rewards, or reward prediction. As pointed out by O'Doherty (2004), it is more likely that reward-related behaviors are not supported by any of these areas in isolation, but depend rather on interactions among them, particularly when the rewards are of a more complex abstract nature. Also, it is becoming clear that some of the structures involved in reward processing, like the ACC or the amygdala, are further composed of subdivisions with different functional properties, and that each of these subdivisions maybe involved in a different aspect of reward processing. Recent studies have also reported reward-related activity in other areas not associated traditionally with reward such as the brainstem (Pecina et al. 2006). Further work is needed to explore these possibilities.

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CHAPTER 3

A CRITICAL ANALYSIS OF THE NEUROPHYSIOLOGICAL LITERATURE ON THE EFFECTS OF POSITIVE AFFECT ON COGNITION

Types of ERP Components and Their Meaning

Before analyzing the ERP and fMRI literature on positive affect, it may be useful to briefly review some of the types of ERP components that have been observed when studying brain activity during affective states or in response to affective stimuli. One such component is the N400. It represents a negative deflection in the brain's electrical field which occurs between about 300 – 500 ms after stimulus onset, peaking at about 400 ms. The N400 is typically demonstrated in sentence-reading tasks in which the last word completing a sentence is semantically incongruent (unexpected) (Kutas and Hillyard 1980a). Semantically incongruent words are found to elicit larger N400 than semantically congruent words and the magnitude of the N400 is proportional to the degree of semantic deviation of a stimulus from its context (Kutas and Hillyard 1980a). Stimuli that are incongruent with one's current emotional state have also been found to elicit a larger N400 than emotionally congruent stimuli (Chung et al. 1996; Kiefer et al. 2007). Another ERP component that inexes unexpectedness is the P300 - a positive deflection in the brain's electrical field that peaks at about 300 ms after stimulus onset. While the N400 reflects semantic deviations from expectancy, the P300 indexes perceptual unexpectedness (e.g., a word in a font larger than the rest of the text, a high-pitch tone in a series of low-pitch tones). Other ERP components that have been observed when studying brain activity during affective states or in response to affective stimuli include a series of early

positive and negative potentials which occur immediately after stimulus onset (100-200 ms), as well as a series of late positive potentials (LPPs) that occur about 500 to 700 ms after stimulus onset. The early ERPs are typically associated with early discrimination of and attention to a stimulus, while the LPPs are thought to reflect cognitive processing required for sustained attention, stimulus evaluation, or memory encoding (Herbert et al. 2008).

Processing of Affective Stimuli

Researchers have used electrophysiological measures to get an insight into how the brain processes various affective stimuli such as images or words. While these studies do not deal with affective states, they are useful because they reveal how the brain processes affective cues that may induce temporary affective states such as positive or negative moods. In fact, various affective stimuli such as pleasant pictures or words have been used to induce positive affect in people (Federmeier et al. 2001; Isen et al. 1985).

A series of ERP studies examined changes in brain activity while participants viewed various positive, negative, and neutral-valence images (Cuthbert et al. 2000; Junghöfer 2001; Schupp et al. 2000). A common finding in all these studies is that emotional pictures (either positive or negative), relative to neutral pictures, induce increased early posterior negativity (EPN), late positive potential (LPP), and a sustained slow wave of positive potentials. The enhanced EPN to positive and negative images is interpreted to index an advantage in early perceptual encoding of emotional stimuli over neutral ones (Schupp et al. 2006). The increased LPP amplitude to emotional stimuli has been suggested to reflect their sustained representation in working memory, indicating a greater intrinsic significance of

emotional over neutral stimuli (Schupp et al. 2006). The extended positive slow wave observed during the viewing of emotional images in some of these studies (e.g., Cuthbert et al. 2000) has been associated with a more elaborate processing of emotional relative to neutral images. Overall, researchers have concluded that the consistent modulation of ERP components by emotional images indexes preferential attending and processing of such stimuli over neutral ones, regardless of valence.

One problem with these studies, however, is that affect is confounded with arousal. In all of them, the positive and negative images used are both significantly more arousing than the emotionally neutral images. For example, in Cuthbert et al. (2000) and in Schupp et al. (2000) target images were selected from the International Affective Picture System (IAPS; Lang et al. 1999) and the emotional pictures were of highly arousing content (e.g., spiders, mutilations in the negative-valence set; sports, nudes in the positive-valence set). The images were presented in random order and participants were asked to report their reactions to each image on scales measuring affective valence and arousal. Physiological and ERP measures were recorded simultaneously. The observed pattern of enhanced amplitude of ERP components described earlier was correlated with participants' self-reported ratings of experienced affect and arousal and with measures of skin conductance. Thus it is not clear whether the observed modulation of brain activity by emotional stimuli in these studies indexed affective valence or arousal. In the affect literature, valence (or pleasantness) and arousal have been conceptualized as orthogonal components of affect (Mano 1997; Russel 1980) and behavioral studies have shown that positive affect and affectless arousal have distinct effects on cognitive processes (Isen, Daubman, and Nowicki 1987). Only by disentangling the two would one be able to conclude that the observed ERP modulations reflect an attentional and processing advantage of affective stimuli. Furthermore, taking arousal out of the picture may reveal differences in

response to positive and negative stimuli that may have been obscured. For example, it may be that positive and negative images are differentially discriminated (as would be indicated by differences in early ERP latencies) or elaborated (as would be indicated by differences in LPP amplitude). A study designed with low-arousal positive and negative images would make it possible to answer these questions more clearly.

Electrophysiological measures of responses to affective cues have also been recorded using verbal stimuli (e.g., words). For example, Herbert et al. (2008) recorded ERPs while participants read pleasant, unpleasant, and neutral adjectives. At the end of the study, participants were given a surprise free-recall test. Memory performance differed as a function of word valence: pleasant adjectives were remembered significantly better than neutral adjectives, while recall of unpleasant and neutral words did not differ.

Electrophysiological data showed that positive and negative adjectives elicited significantly larger-amplitude early negative potentials relative to neutral adjectives, indicating again an attentional advantage of emotional over neutral stimuli. Positive and negative adjectives (relative to neutral adjectives) elicited also larger N400 potentials. Importantly, the N400 potential was smaller for positive relative to negative adjectives, indicating facilitated semantic integration of pleasant relative to unpleasant material, consistent with the behavioral data. Positive and negative adjectives also elicited significantly different late positive potentials: positive adjectives elicited larger LPPs compared to negative adjectives. In fact, LPPs for negative and neutral adjectives did not differ, but pleasant adjectives induced significantly larger LPPs than either neutral or unpleasant adjectives. As mentioned earlier, LPPs are thought to reflect cognitive processing required for sustained attention, stimulus evaluation, or memory encoding. Thus larger LPPs for positive stimuli may imply that pleasant information is selectively attended and elaborated

relative to unpleasant or neutral information, as has been suggested before (Isen 1984) and as indicated also by the better recall for pleasant words in this study.

In sum, electrophysiological measures of responses to emotional stimuli suggest that such stimuli are processed preferentially over nonaffective stimuli. When the stimuli are highly arousing images, no difference is observed between responses to negative and positive emotional images. However, when the stimuli are more abstract (words), a facilitated processing of positive stimuli is observed, reflected in a reduced-amplitude N400 to positive relative to negative words. Positive words are also elaborated more relative to negative or neutral words, as indicated by an enhanced LPP component. It is not quite clear why the ERP differences between positive and negative stimuli were observed for words but not for images, since the emotional words used in the Herbert et al. (2008) study were also significantly more arousing than the neutral words. It may be that although valence was still confounded with arousal in the word study, words are overall of a more abstract nature than images and this makes it possible to observe the difference in response to positive and negative stimuli. Studies with either images or words designed so that affect is not confounded with arousal could shed more light on these processes.

ERP and fMRI Evidence for the Interplay between Affect and Cognition

A series of studies using ERP and fMRI methods have been designed to shed light on issues related to the interplay between affect and cognition. We review here several studies that address questions related to the impact of affect on memory and on processes related to flexible thinking and creativity.

The Influence of Affect on Memory

It has long been recognized that affect influences memory processes and that the current affective state of a person modulates the type of material retrieved from memory as well as judgments made about stimuli. For example, in several studies by Isen and colleagues (Isen and Shalker 1982; Isen et al. 1978), individuals in whom positive affect had been induced gave more favorable evaluations of neutral (but not negative) items relative to individuals in a neutral affect condition. It was suggested that positive affect has these effects because it serves as a cue that makes positive material more accessible from memory (Isen et al. 1978).

Proponents of the "affect-as-information" hypothesis (Schwarz 1990; Schwarz and Clore 1983), on the other hand, have argued that the effects of positive affect on memory and judgments are the result of a different type of mechanism. They have suggested that when making evaluations, people ask themselves how they feel about the object of judgment. The experience of positive affect is interpreted to mean that the object is valuable, which leads to a positive judgment, and the experience of negative affect is interpreted to mean that the object of judgment lacks value, leading to a more negative judgment. It has also been suggested that negative affect signals the existence of problems that need to be solved and motivates careful systematic processing, whereas positive affect signals that the environment is benign and encourages sloppier, less careful processing as there is no need to exert cognitive effort (Schwarz and Clore 1983).

A significant amount of behavioral data has accumulated that is inconsistent with this position. For example, a series of studies by Isen and colleagues on decision making have shown that positive affect promotes the use of more efficient decision-making strategies without leading to the use of heuristics or to sloppier thinking (Estrada, Isen, and Young 1997; Isen, Rosenzweig, and Young 1991). Also, studies

have shown that people in positive affect (relative to those in neutral affect) are more likely to attend to and elaborate on negative information when it is important and self-relevant (Reed and Aspinwall 1998; Trope and Pomerantz 1998). Furthermore, evidence that positive affect leads to less careful processing is usually indirect (see, e.g., Isen 2000, for discussion). In persuasion studies, for example, positive affect participants have been shown to change their attitude following either weak- or strong-attitude messages, while neutral- or negative-mood participants are persuaded only by the strong-argument message. However, as pointed out earlier (e.g., Isen 2000), when explicitly asked, positive affect participants do distinguish between strong and weak arguments, and they also don't differ from controls in memory for the content of the message (Bless et al. 1990; Mackie and Worth 1989). Finally, Bless et al. (1996) showed that although participants in positive affect made more intrusion errors in a recognition task, implying greater reliance on general knowledge structures, they also performed significantly better than negative-mood participants on a secondary cognitive task, providing evidence against the hypothesis that positive mood leads to cognitive or motivational impairment.

In spite of all this evidence, the position that positive affect leads to less systematic processing and to reliance on heuristics has been slow to loose ground. For example, only recently Clore and Huntsinger (2007) reviewed literature in support of the idea that positive affect leads to more stereotyping, false memories, and use of heuristics, and that it influences memory and judgments directly by serving as "experiential and bodily information regarding how one feels about the object of judgment" (Clore and Huntsinger 2007, p. 393). It is insightful, therefore, to look at electrophysiological and imaging data that might shed light into the mechanisms through which positive affect influences memory and judgments.

The influence of affect on mechanisms of retrieval. Chung et al. (1996) investigated how mood states influence the semantic material activated from memory. This was done by recording ERP responses to good or bad outcomes of various life stories that were congruent or incongruent with participants' experimentally induced affective state. Affect was induced by informing participants that they would be in charge of their own mood state and that they had been randomly assigned to either a "pessimistic" or an "optimistic" mood condition and should maintain this mood by thinking about happy or sad events in their life. Subsequently, participants read brief stories of life events. They had to press a key to read the last word of the story which represented the story outcome and was either good (happy outcome), bad (sad outcome), or semantically incongruent.

Semantically incongruent outcomes elicited the largest N400 potentials. This is consistent with previous findings (Kutas and Hillyard 1980 a, b) indicating that N400 amplitude indexes semantic deviations from expectations. Importantly, mood-incongruent outcome words were also associated with an N400 that was reliably larger than the N400 for mood-congruent words, although smaller than the N400 for semantically incongruent words. Specifically, bad outcomes elicited larger N400 than good outcomes for participants in the optimistic-mood condition and conversely, good outcomes elicited a larger N400 than bad outcomes in participants in the pessimistic mood condition. Thus, just as material that was semantically incongruent with its context elicited large N400, so did material that was incongruent with mood in terms of affective valence. This implies that different mood states activated different types of material from memory, which is consistent with Isen et al.'s (1978) suggestion that positive mood brings to mind positive material from memory.

Chung et al. (1996), however, found symmetric effects for pessimistic and optimistic moods: pessimistic mood made negative outcomes more accessible as

reflected in the smaller N400 for negative outcomes relative to positive outcomes. Results for the effect of negative mood on memory have been mixed. While findings from studies with depressed individuals suggest that negative mood produces biases in favor of negative material in memory (see Chung et al. 1996 for a review), in a study by Isen et al. (1978) negative mood did not enhance memory for previously learned negative words relative to neutral words (Isen et al. 1978). The results from Chung et al. (1996) should be interpreted with caution. First, they did not directly test memory; although the ERP data suggests that the different mood states activated different type of semantic material from memory, we do not know if mood also influenced recall. Second, the mood manipulation technique used in the study was rather heavy-handed. Participants were explicitly told that they had to maintain a particular mood during the study and that they were to expect an outcome to each of the life stories that was either emotionally good or bad. It is possible that this manipulation created a demand effect and participants were aware that if they were in an optimistic state they should expect a good outcome, and if they were in a pessimistic state they should expect a bad outcome. A replication of the Chung et al. (1996) study with a proper affect induction would help clarify the effects of positive and negative affect on access to material in memory.

Recently, Kiefer et al. (2007) conducted a study with a more subtle manipulation of affect that examined the influence of affect on the type of semantic material retrieved from memory and on memory at encoding. The focus of the study was on ERP patterns observed while participants in either positive or negative affect learned lists of emotional words. The dependent measures of interest were ERP deflections during encoding of the words, as well as behavioral measures such as recall performance, as a function of mood and word valence. Half of the words participants had to learn were fragmented (had 1 to 3 letters missing). This was done

to explore the effect of affect on memory when information is actively manipulated during encoding (by generating the word from the word fragment). The researchers hypothesized that mood states would activate mood-congruent material in memory providing a semantic context for the words to be encoded. Words of valence congruent with the induced mood were expected to elicit smaller N400 amplitude than incongruent words, since N400 is typically smaller when the semantic material is already activated by a preceding semantic context (Kutas and Hillyard 1980a, b). Affect in this study was induced by having participants view a series of short video clips (with either funny or sad content) prior to learning the word lists. Words were positive or negative trait adjectives that were equated on frequency and length and were also of very low arousal (.30 to .99, on a scale of 1 to 5). During the learning task, words appeared on a computer screen one by one, each followed by a blank screen, and then a question mark at which point participants were asked to say aloud the word they had just seen. At the end of each word series, participants performed a free-recall task and reported the strategy they had used during learning.

ERP data revealed a main effect of word valence: positive words elicited smaller N400 than negative words. More importantly, this main effect of stimulus valence was modulated by participants' affective state. Positive words elicited a significantly smaller N400 than negative words only in participants in positive affect; for participants in negative affect the effect of word valence was absent - there was no significant difference in N400 amplitude for positive vs. negative words. These results imply that positive mood may have activated stored positive semantic material in memory and as a result, mood-congruent (positive) words were primed and were more efficiently encoded into existing knowledge structures. This replicates the effect of positive mood obtained by Chung et al. (1996) and provides indirect evidence against the "affect-as-information" position that positive affect influences judgments directly

through a heuristic inference from the current mood ("how do I feel about it?"), rather than through integration of the incoming information into activated semantic structures. Unlike Chung et al. (1996), however, Kiefer et al. (2007) did not observe a reciprocal effect for negative affect. While positive affect facilitated the encoding of positive emotional words, negative affect did not conversely facilitate the encoding of negative words. It is possible that this asymmetry was not observed in Chung et al. (1996) due to the heavy-handed nature of their affect induction, while Kiefer et al. (2007) used a more subtle affect induction.

Further support for the asymmetry between the effects of positive and negative affect came from source analysis of the ERP data. This analysis revealed that negative affect was associated with activity in the dorsolateral prefrontal cortex, an area associated with working memory processes during rote rehearsal, and the right inferior prefrontal cortex, an area associated with negative emotions (Kiefer et al. 2007). Positive affect, on the other hand, was associated with activity in the left inferior prefrontal cortex and also with activity close to the frontal midline. The left inferior prefrontal cortex is a region that has been involved in verbal information processing during episodic memory. Activity close to the frontal midline is attributed to activation of the dorsal parts of the anterior cingulate cortex – an area that has been implicated in executive control processes and in the flexible updating of cognitive representations (Bush, Luu, and Posner 2001; Ashby, Isen, and Turken 1999). These results are in line with the dopaminergic hypothesis of positive affect (Ashby et al. 1999) which holds that the effects of positive affect on cognition are mediated by increased release of the neurotransmitter dopamine in areas such as the prefrontal cortex and the anterior cingulate. They also provide evidence against the position that positive affect leads to a heuristic non-systematic cognitive style while negative affect promotes a more analytical and careful processing (Mackie and Worth 1989; Schwarz

and Bless 1991). The behavioral data in the study further strengthens these findings. Specifically, recall rate was highest for positive generated words in participants in positive mood. Also, participants in positive mood reported most frequently using elaborative strategies when learning the words (i.e., forming a story out of the word, relating it to a familiar person), characteristic of deeper semantic encoding. Participants in negative affect, on the other hand, reported using non-elaborative strategies such as rote rehearsal most frequently.

In sum, the electrophysiological data reported by Chung et al. (1996) and Kiefer et al. (2007) provide insights into several important issues related to positive affect (see Isen, 1984, 2000 for discussion of the issues). First, they provide evidence at the neurological level that positive affect makes positive material more accessible in memory. Second, they reveal an asymmetry between the effects of positive and negative affect on cognitive processes. Third, they provide support for the position that positive affect does not lead to non-systematic careless processing but rather promotes an elaborative cognitive style, that is at least in part mediated by activity in dopamine-rich areas such as the prefrontal cortex and the anterior cingulate.

Neither Chung et al. (1996), nor Kiefer et al. (2007) included a control neutral-affect condition in their studies. Adding such a condition is important, because the study by Herbert et al. (2008) reviewed earlier revealed smaller N400 for positive relative to negative adjectives even in participants in neutral mood. Thus one may argue that people normally process pleasant positive-valence information more easily than negative information and that the attenuation of N400 amplitude for positive stimuli observed by Chung and Kiefer may just as likely be observed in neutral-affect condition. Including a neutral-affect condition and comparing the amplitude of the N400 in that condition to the N400 in the positive-affect condition would make it

possible to conclude with more certainty that positive affect cues positive material and facilitates its semantic integration in memory.

The influence of affect on mechanisms of encoding. The pattern of results observed by Kiefer et al. (2007) suggests that the influence of positive affect on memory can be accounted for not only by mechanisms at time of retrieval, but also by mechanisms at time of encoding. Evidence in this regard from behavioral studies has been mixed. While in some studies participants who learned a list of brand names while being in a positive affective state subsequently recalled more brand names than participants who learned the names in a neutral affective state (Lee and Sternthal 1999), other researchers have found that positive affect impacts memory at time of retrieval but not at time of encoding (Isen et al. 1978). Several studies employing fMRI imaging techniques explore these questions (Erk et al. 2003; Lewis et al. 2005; and Maratos et al. 2001).

Erk et al. (2003) studied the influence of affective context on the encoding of emotionally neutral material. They used fMRI to record brain activity at encoding and correlate it with recall performance. The hypothesis was that differences in recall would be associated with different patterns of brain activation during encoding, as a function of affective state during encoding. Affect in this study was manipulated by having participants view positive, negative, or neutral pictures from the IAP system (Lang 1999). Pictures of a certain valence were grouped in blocks of seven. After the presentation of each picture, a word was shown that had to be classified as abstract or concrete. At the end of each session, participants were asked to recall the words they had seen. Behavioral results indicated that words presented in a block of positive pictures were recalled significantly better than words presented in a block of neutral or negative pictures. Thus positive affect at encoding improved subsequent recall. This is in line with Kiefer et al. (2007) who also found a facilitating effect of positive affect

during encoding on recall performance, and in general with the view expressed by Ashby et al. (1999) of positive affect facilitating a more deep semantic processing of information. The inclusion of a benchmark neutral-affect condition complements nicely Kiefer et al.'s results, indicating a clear encoding advantage under positive affect. Analysis of the fMRI data revealed an overall correlation between recall success and activity at encoding in the left inferior frontal cortex - the same region that was activated when participants in the Kiefer et al. (2007) study encoded words in the positive affect "generate" condition. Researchers have suggested that this region is involved in verbal information processing during episodic memory (Fletcher, Shallice, and Dolan 1998). The relation between recall success and brain activity at encoding, however, was modulated by affect at encoding. Specifically, recall success was associated with activity in the anterior and posterior parahippocampal gyrus and the extrastriate visual areas during encoding in positive affect. When participants experienced negative affect at encoding, recall success was predicted by encoding activation in the amygdala region. These results imply that positive and negative affect activated different brain regions and had their effect on memory through distinct neural mechanisms.

While Erk et al. (2003) and Kiefer et al. (2007) explored the effect of affect on memory by exploring the relationship between brain activation during encoding and subsequent recall, Maratos et al. (2001) examined brain activation at time of retrieval. The material to be encoded in their study were neutral words which were presented in the context of 45 separate sentences: 15 negative, 15 positive, and 15 neutral sentences, mixed randomly. The target neutral word in each of the sentences was presented alone after the sentence, and participants were asked to remember it in the context of the preceding sentence. At the end of the study session participants performed a recognition memory test in which the target words from the study

sentences were presented along with 15 new words. Participants were asked to judge whether or not they had seen each of the words in the study phase. Patterns of brain activation were recorded during the recognition task. Behavioral data did not reveal any differences in recognition as a function of the valence of word context. The lack of difference in memory performance for positive and negative material may be due to the nature of the memory test used - recognition instead of recall. fMRI results showed that retrieval of items encoded in emotional (relative to neutral) contexts was associated with activation mainly in the prefrontal cortex and the hippocampus. Relative to items from neutral contexts, items from positive contexts elicited enhanced activity mainly in the bilateral orbitofrontal cortex which is consistent with evidence that this region is involved in the processing of rewards and reward-predicting stimuli (Rolls 2004; Rolls et al. 2003). Items from the negative contexts elicited activity mainly in the left amygdala. Based on these patterns, Maratos et al. (2001) concluded that re-exposure to previously learned material activated memory for the affective context in which this material was first encoded, implying that the same regions that are activated when emotional information is encoded are also active when emotional information is retrieved from memory. This suggests that semantic material is encoded, among other things, according to its affective valence. This would also imply that a subsequent affective state that is congruent with the valence of the encoded information should facilitate retrieval of this information.

This prediction was tested by Lewis et al. (2005). They examined brain activity, using fMRI, during both encoding and retrieval phases of a mood-congruent memory task. It was predicted that mood at retrieval would reactivate emotional responses linked to the valenced information at encoding. Thus, increased activation in emotion-related areas of the brain during both encoding and retrieval would be associated with facilitative effects of mood congruence on memory. Participants in the

study were first presented with positive and negative words, in mixed order, and asked to indicate whether these words could be used to describe themselves in any abstract sense. Then participants underwent a mood induction procedure involving happy or sad pieces of music played for 3.15 min. accompanied by the presentation of a series of standardized faces with matching emotion (happy or sad). Finally, participants performed a memory test in which they saw a series of words and were asked to indicate which of these words they had seen at study. Brain activity was recorded using fMRI during both the study and the recognition phases of the experiment. The behavioral data showed a significant main effect of word valence: positive words were better remembered than negative words. There was also a trend toward a main effect of word congruence, and a significant interaction between the two. Specifically, there was a significant influence of congruence on memory for negatively valenced words, but not for positively valenced words. Imaging results revealed two brain areas where activity at encoding predicted subsequent mood congruent retrieval and which were also active in response to congruent mood at retrieval. These two areas were the subgenual cingulate for positive valence and the posterior-lateral orbitofrontal cortex for negative valence. The subgenual cingulate has been shown to respond to various stimuli among which are rewards, while the posterior-lateral orbitofrontal cortex has been implicated in punishment (Lewis et al. 2005). Activity in these two areas during encoding predicted subsequent memory in congruent (vs. incongruent) moods, and they also exhibited greater activation during congruent (vs. incongruent) recall.

The results of the Lewis et al. study imply that semantic material is encoded, among other aspects, according to its valence and that a congruent mood at retrieval facilitates recollection of this material. Isen et al. (1978) had previously suggested that material to be learned is encoded according to its semantic meaning (including its valence) and that material of positive semantic meaning is more readily accessed later

in a congruent positive mood. Lewis et al., however, propose that mood-congruence effects can be due to any factor influencing encoding: not just the semantic meaning of the material, but also mood, arousal, etc. This proposition is consistent with the state-dependent learning paradigm, whereby memory is facilitated when mood at retrieval matches mood at encoding. The behavioral data by Isen et al. (1978) speak against state-dependent learning. In their studies, performance at retrieval was not influenced by mood at encoding, but only by mood at retrieval, and the congruence between affective state during the two stages (encoding and retrieval) did not impact memory. To test the validity of the proposition by Lewis et al., (2001) using imaging data, a study would have to be designed in which affect is manipulated both at encoding and at retrieval, and brain activity is also recorded at both points in time. Evidence in support of state-dependent learning would be obtained if, behaviorally, recall is facilitated when mood at encoding matches mood at retrieval. At the neurological level we would expect to see enhanced activation of brain areas implicated in positive or negative affect during both encoding and retrieval.

The Influence of Affect on Cognitive Flexibility and Creativity

Behavioral studies have shown that positive affect promotes cognitive flexibility. Specifically, people in positive affect, relative to those in neutral affect, have been shown to give more diverse and less typical associations to neutral words (Green and Noice 1988; Isen et al. 1985) and to categorize neutral material more flexibly and see more ways in which nontypical members of categories can fit or be viewed as members of these categories (Isen and Daumban 1984; Isen, Niedenthal and Cantor 1992; Kahn and Isen 1993). The enhanced cognitive flexibility under positive affect has also been shown to lead to increased creativity and problem solving abilities (Estrada, Isen, and Young 1997; Isen, Daumbman and Nowicki 1987; Isen and Means

1983). Isen and colleagues have suggested that positive affect has these effects because it cues access to positive material in memory (Isen et al. 1978) and positive material in memory is richer than neutral material (Boucher & Osgood 1969; Isen et al. 1985). Therefore, positive affect creates a richer cognitive context which allows people to think of more and more unique aspects of things and to see more relationships and associations between them. This leads to a more flexible categorization of items, whereby individuals in positive mood, compared to those in neutral mood, are more likely to classify fringe exemplars of a category as members of that category and in general to find more relationships and associations between distantly related items (e.g., Barone, Miniard, and Romeo 2000; Isen and Daubman 1984; Isen, Niedenthal & Cantor 1992; Kahn and Isen 1993). Studies by Federmeier et al. (2201) and Subramaniam et al. (2008) explore the neurological mechanisms behind these effects.

Federmeier et al. (2001) used ERP methodology to examine the influence of positive affect on accessibility of material in memory and on cognitive organization. In this study, positive affect was induced by having participants view a series of "happy" photographs (e.g., cute animals, smiling people), while controls viewed photographs of neutral objects (e.g., household objects, etc.). All photographs were selected from the IAPS (Lang et al. 1999) and positive and neutral photographs did not differ in terms of arousal. In the main task, participants viewed pairs of sentences on a computer screen; the first sentence established the context for the follow-up target sentence. The target sentence was presented word by word and the last word differed in the extent of its expectancy or congruence with the preceding material. For example, the context sentence 'They wanted to make the hotel look more like a tropical resort' was followed by the target sentence 'So, along the driveway they planted rows of…' which ended either with "palm trees" (expected), "pine tress"

(unexpected but from the expected semantic category), or "tulips" (unexpected and from a different, thought related semantic category). ERP results indicated that both controls and positive-affect participants exhibited comparable large N400 amplitude following the unexpected word from the same category (pine trees) relative to the expected word (palm trees), indicating that the unexpected word was harder to integrate semantically than the expected word. However, controls exhibited an even larger N400 following the incongruous exemplar from the different category (tulips), while for participants in positive affect the N400 amplitude following the unexpected but related category exemplar (tulips) was not larger than that following the unexpected same-category exemplar (pine trees). These results were interpreted to imply that positive mood, relative to neutral mood, facilitated the integration of exemplars from distantly related categories.

However, one may argue that the attenuated N400 amplitude in the positive affect condition indicates less careful processing of the material, rather than facilitation of the semantic integration of distantly related items. It may be that participants in positive affect did not perceive differences between unexpected target and non-target items because they processed the information more superficially and registered only the obvious discrepancy (between the expected and unexpected items) but did not appreciate the difference between unexpected items that came from different categories. Such an interpretation would be consistent with the position, described earlier, that positive affect leads to increased use of heuristics and to less careful and systematic processing of information due to reduced cognitive or motivational capacity (e.g., Bless et al. 1990; Mackie and Worth 1989; Schwartz and Clore 1983). A modified version of the Federmeier et al. (2001) study can be designed to rule out such an interpretation. Specifically, in addition to the three types of sentence endings used in the original study, a fourth type of sentence ending could be

added – unexpected and from a category completely unrelated to the target one. If positive affect leads to less careful processing, then under positive affect the amplitude of the N400 component in response to the unexpected and unrelated-category item would not differ from the N400 to the other two unexpected items. However, if positive affect helps people to see associations between more distantly related items, but not between completely unrelated items, then under positive mood N400 to unexpected unrelated items would be larger than N400 to unexpected but plausibly related items. Furthermore, including a negative-mood condition would also allow us to compare the effect of positive and negative affect on semantic organization and memory retrieval processes.

A recent fMRI study by Subramaniam et al. (2008) also explores the neurological mechanisms through which positive affect promotes cognitive flexibility. The study examines the relationship between affect and problem solving strategy (insight vs. analytical) on the one hand, and affect and brain activity immediately prior and during problem solving, on the other hand. Participants in this study were given a set of Remote Associates problems which could be solved applying either a creative "insight" strategy, or a more methodical and analytic strategy without insight. Affect was not experimentally induced, but was measured at the beginning of the session through self-reports on the positive and negative affect scale (PANAS) and state anxiety scale (STAI). For each problem, participants indicated the type of solution strategy they had used. Brain activity was recorded, using fMRI, prior to as well as during problem solving.

Behavioral results showed that participants higher in positive affect solved significantly more problems, and in particular solved more problems using an insight strategy, relative to participants lower in positive affect. Positive affect did not influence the number of problems solved analytically.

fMRI data indicated that the creative problem solving advantage under positive mood was mediated by activity in the dorsal anterior cingulate cortex. Specifically, preparatory activity (activity immediately before problem presentation) in the dorsal anterior cingulate cortex correlated with positive affect and with dorsal anterior cingulate activity during "insight" problem solving. This is in line with Ashby et al.'s (1999) dopaminergic account for the effect of positive affect on creativity and cognitive flexibility in general. In particular, Ashby et al. (1999) have suggested that positive affect's beneficial influence on cognitive flexibility is at least in part mediated by enhanced release of the neurotransmitter dopamine in brain areas including the anterior cingulate cortex. The anterior cingulate is involved in executive control processes, and in particular in the selection of cognitive perspective. It has been hypothesized that increased dopamine levels in the anterior cingulate enhance cognitive flexibility by facilitating the selection of more unusual responses over prepotent, more dominant responses. This is precisely the type of mechanism involved in "insight" problem solving where the right solution is reached by perceiving relationships and associations between more distant and not obviously related concepts.

The study by Subramaniam et al. (2008) is important because it provides direct neurological evidence in support of Ashby et al.'s (1999) dopaminergic hypothesis of positive affect. Importantly, participants high in positive affect did not solve fewer problems using analytical strategies relative to those low in positive affect, but they also solved significantly more problems through a more creative insight process. This implies that the creative problem solving advantage observed under positive affect did not come at the cost of more systematic analytical problem solving. Furthermore, anxiety had the opposite effect: participants higher in anxiety solved as many problems using analytical strategy as people lower in anxiety, but they solved

significantly fewer problems with insight. Thus neither positive mood nor anxiety influenced analytical problem solving, but they had significant and opposite effects on creative problem solving.

Summary and Implications

The ERP and imaging studies reviewed in this paper provide insight into a number of areas related to the effect of positive affect on cognitive processes. First, Chung et al. (1996) and Kiefer et al. (2007) show that positive affect facilitates the processing of positive-valence stimuli, as indicated by a smaller N400 component for positive material under positive affect. This is consistent with behavioral data suggesting that positive affect makes positive material more accessible from memory (Isen et al. 1978). Federmeier et al. (2001) further provide evidence that positive affect, relative to neutral affect, activates more diverse semantic material from memory and creates a richer cognitive context that allows people to perceive associations and relationships between more distantly related items. This is indicated by a smaller N400 ERP component in response to exemplars of distant but plausibly related semantic categories observed in conditions of positive (relative to neutral) affect. These findings are in line with behavioral data suggesting that positive affect helps people think of more unique and diverse associations to words and facilitates a more flexible categorization of semantic material (e.g., Isen and Daubman 1984; Isen et al. 1985). Neurological evidence for the effect of positive affect on cognitive flexibility comes also from the study by Subramaniam et al. (2008) who demonstrate that people high in positive affect are just as good as those low in positive affect at solving problems through analytic strategy, and are significantly better at solving problems through creative "insight" strategy. It is also shown that these effects are

associated with activity in the dorsal anterior cingulate cortex, an area that has been implicated in cognitive control processes.

The studies also reveal that the effects of positive affect on memory are not limited only to processes at retrieval. In Kiefer et al. (2007) participants exhibited superior recall and reported using learning strategies indicative of more elaborate deep processing when they had encoded material under positive (vs. negative) affect. This superiority of positive affect was correlated with activity (during encoding) in the left inferior prefrontal cortex and the dorsal anterior cingulate cortex, indicating again the presence of more complex processing under positive affect.

Overall, the ERP and fMRI data from the examined studies is in line with a growing number of behavioral studies showing that positive affect promotes flexible and creative thinking, without leading to less careful processing or to increased use of heuristics (e.g., Ashby et al. 1999; Bauman and Kuhl 2005; Estrada et al. 1997; Fredrickson and Branigan 2005; Isen et al. 1987; Reed and Aspinwall 1998). The papers also provide evidence that the effects of positive and negative affect on cognition are not symmetrical: while positive affect cues positive material from memory, negative affect does not cue negative material from memory and does not facilitate the integration of such material, at least not in healthy subjects (Isen 1984, 1990; Isen et al. 1978; Kiefer et al. 2007). It is possible that the tendency for people in negative affect to skew thinking towards negative content in memory reported elsewhere (see Chung et al. 1996 for a review) is limited to patients suffering from depression. Future ERP studies with such groups of participants could test for this possibility. The reviewed studies also show that negative affect does not improve analytical and systematic thinking (Subramaniam et al. 2008) and that it leads to the use of more shallow learning strategies such as rote rehearsal (Kiefer et al. 2007). These results are in sharp contrast to the position held by proponents of the affect-as-

information model (Schwarz and Bless 1991; Schwarz and Clore 1983) who argue that negative mood promotes careful systematic thinking (e.g., Clore and Huntsinger 2007; Gasper and Clore 2002; Storbeck and Clore 2005). Finally, studies using fMRI technology demonstrate that positive and negative affect are associated with activity in different brain areas: negative affect is consistently associated with activation of the amygdala, while cognitive effects under positive affect are associated with activity in various areas among which the dorsal anterior cingulate cortex and the left inferior prefrontal cortex.

Some areas remain to be clarified. First, most of the studies reviewed did not include a control neutral-affect condition. As explained earlier, this poses a problem as conclusions are drawn based on comparison of effects under positive affect with those under negative affect and it is not clear whether observed differences are due to the effect of positive (relative to neutral) affect, the effect of negative (relative to neutral) affect, or both. Also, positive affect is sometimes confounded with arousal, which also makes drawing conclusions about the causality of the observed effects difficult.

In terms of theoretical implications, several questions come to mind. For example, in Isen et al. (1978), affect at time of encoding did not affect the material to be learned. Erk et al. (2003) and Kiefer et al. (2007), on the other hand, showed superior recall for words learned in positive affect. It may be that Isen et al. (1978) did not observe a memory effect of affect during encoding because affect was manipulated both at encoding and at retrieval.

Another question that remains to be clarified relates to state-dependent learning. Although none of the studies reviewed here tested directly for state-dependent effects, Lewis et al. (2005) suggested that just as congruence between valence of encoded material and affect at time of retrieval improved memory, so would congruence between affect at time of encoding and affect at time of retrieval. A

study that manipulates affect at both points in time, and also records brain activity at both points in time could test this prediction.

Finally, an issue that needs clarification concerns the brain areas that were found to be involved in mood-congruency memory effects. Erk et al. (2003), on the one hand, reported that memory performance was correlated with encoding activity (under positive mood) in the anterior and posterior parahippocampal gyrus and the extrastriate visual areas. Lewis et al. (2005), on the other hand, found that memory performance was predicted by encoding activity (under positive mood) in the subgenual cingulate. The difference may be due in part to differences in the nature of the stimuli to be encoded: neutral words in the Erk study, and positive and negative words in the Lewis study.

In closing, the studies reviewed in this paper provide support at the neurological level for the beneficial effects of positive affect on thinking and behavior demonstrated previously (see Ashby et al. 1999; Isen 2000, 2008 for reviews). Future ERP and fMRI studies could further enhance our understanding of the specific mechanisms that underlie the wide range of cognitive and behavioral effects of positive affect.

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